Bulletin

of the

Torrey Botanical Club

VOLUME 70

FOUNDED BY WILLIAM HENRY LEGGETT 1870

Editor

Harold W. Rickett

NEW YORK

1943

Published for the Club
by
THE SCIENCE PRESS PRINTING COMPANY
LANCASTER, PENNSYLVANIA

CONTENTS

Dates of Issue of Volume 70

Number 1, for January	December 31, 1942
Number 2, For March	March 2, 1943
Number 3, for May	April 30, 1943
Number 4, for July	July 12, 1943
Number 5, for September	September 1, 1943
Number 6, for November	November 16, 1943

ERRATA

p. 44, No 7 in key. For *E. elvasoides* read *E. elvasiodes.*
p. 48, l. 34, 35. For *elvasiodes* read *elvasioides.*
p. 79, l. 14. For *Erythrina berteroana* read *Erythrina Berteroana.*
p. 218, l. 10. For *Acer grandidentata* read *Acer grandidentatum.*
p. 222, table 3, l. 11. For *Vitis aestivale* read *Vitis aestivalis.*
p. 233, l. 20. For *Aruncus silvester* read *Aruncus sylvester.*
p. 329, citation 17. For **Hammer** read **Hamner.**
p. 443, citation 24. For **Goodum** read **Goodwin.**
p. 446, citation 3. For **Withdrow** read **Withrow.**
p. 514, l. 12. For *Franklinia altamaha* read *Franklinia alatamaha.*

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 1, pp. 1–14 JANUARY, 1943

THE MICROBIOLOGY OF THE UPPER AIR[1]

FRED T. WOLF

A most important development in the study of microorganisms occurring in the upper air is marked by the work of Stakman et al. (1923), who were the first to make use of the airplane for microbiological work, in collecting fungus spores from altitudes of as much as 16,500 feet. Soon afterward, Mischustin (1926) isolated numerous bacteria upon plates of nutrient media exposed from airplanes above the city of Moscow. Although bacteria, fungus spores, and pollen grains compose by far the greater portion of the aerial flora, the finding of actinomycetes, yeasts, algae, and moss spores (van Overeem, 1936) at considerable altitudes has resulted in the establishment of aerobiology as a fertile field of microbiological research.

The apparatus and techniques employed in collecting and studying organisms from the air have necessarily been diverse. Glass slides coated with vaseline or glycerine jelly and examined microscopically, or Petri dishes containing nutrient media for cultural studies have been used by many investigators. Among the more elaborate appliances that have been devised may be mentioned the ingenious apparatus for use with balloons, developed by Chatterjee (1931), the "sky hook" of Meier and Lindbergh (1935), the parachute apparatus of Rogers and Meier (1936) for collecting bacteria from the stratosphere, the apparatus of van Overeem (1936), and the bioaerocollector of Proctor and Parker (1938). The various types of apparatus, the techniques of using them, and the evaluation of data obtained by their use have been discussed in recent articles on aerobiological methods by Durham (1941) and the Committee on Apparatus in Aerobiology (1941).

The results of efforts to collect microorganisms from air over the ocean remote from land (Bisby 1935; Meier 1936a; Meier and Lindbergh 1935; Rittenberg 1939; Durham 1941) show that organisms in the air can be transported for long distances. Durham (1938a) has described a movement of air masses in which *Alternaria* spores, originating in Minnesota, were carried to the Atlantic and Gulf coasts in about fifty-five hours, and in which "thousands of tons of mold spores were transported an average distance of several hundred miles."

The practical importance of aerobiological investigations is well illustrated in the field of plant pathology by studies of spore dissemination in the cereal rusts made by Stakman et al. (1923), Craigie and Popp (1928).

[1] Paper presented before the Association of Southeastern Biologists in Miami, Florida, on April 17, 1942.

[THE BULLETIN for December (69: 627–711) was issued December 2, 1942]

Peturson (1931), and Hubert (1932). The incidence of air-borne fungus spores in relation to human allergy has been extensively studied by Durham (1937, 1938a) and others, while studies on air-borne pollen grains in relation to allergic conditions in man are so numerous as to be entirely beyond the scope of this brief review.

Just how far above the surface of the earth living organisms exist is still an unanswered question. Stakman et al. (1923) and Meier, Stevenson, and Charles (1933) report a decided decrease in the number of microorganisms above 8,000–11,000 feet. Walker (1935) failed to find bacteria above an altitude of 19,000 feet. On the other hand Proctor (1934) reported that bacteria and fungus spores were obtained at the greatest altitudes studied by him, namely, at 20,000 feet. Stevens (1936) and Rogers and Meier (1936) reported the isolation of bacteria and fungus spores from the stratosphere at altitudes in excess of 36,000 feet.

In order to remain viable at high altitudes, organisms must be highly resistant to fluctuations in temperature, atmospheric pressure, and humidity, and to exposure to large amounts of ultraviolet radiation (Proctor 1934; Meier 1936b; Jacobs 1939). In spite of these environmental factors unfavorable for microorganisms, a surprisingly large number of forms have been found to occur at considerable altitudes. The bacterial flora of the air has been investigated by Mischustin (1926), Proctor (1934, 1935), Walker (1935), Rogers and Meier (1936), Proctor and Parker (1938), and Rittenberg (1939). Forty-nine species of eight genera, including spore-forming rods, non-spore-forming rods, and cocci have been identified by Proctor et al. The fungus flora of the air is even more diverse, and representatives of some forty genera, chiefly Fungi Imperfecti, but also including rusts, smuts, ascomycetes, and Mucorales, have been found at altitudes of several thousand feet (Brown 1930; Meier, Stevenson and Charles 1933; Proctor 1934, 1935; Meier and Lindbergh 1935; MacQuiddy 1935; Durham 1937, 1938; Tasugi and Kurosawa 1938; Rittenberg 1939).

MATERIALS AND METHODS

The present studies were undertaken in order to determine the kinds of microorganisms present at various altitudes in the air over Nashville, Tennessee, to obtain quantitative data as to relative prevalence of the various kinds, and to attempt to correlate these data with existing weather conditions. Six flights were made from Berry Field, Nashville, during the months of October, November, and December, 1941, and January and February, 1942.

No exposures were made at altitudes of less than 1,000 feet, in order to rule out the rather large amount of contamination from the surface of the earth experienced below this level. The first three flights, on October 19,

October 26, and November 9 were made at comparatively low altitudes of 1,000-2,000 feet, and were of a preliminary nature, devoted to becoming familiar with the manipulation of apparatus, to determining proper times of exposure, and to gaining some indication of types of organisms to be found. On December 6, plates were exposed at intervals of 1,000 feet of altitude (on both the ascent and descent) up to a maximum of 10,600 feet. Similar exposures, at lesser intervals of altitude, up to maxima of 6,000 feet and 3,500 feet were made on January 25 and February 22, respectively.

The technique employed consisted in exposing Petri dishes containing ordinary nutrient agar (beef extract, 3 gm.; Bactopeptone, 5 gm.; agar, 15 gm.; distilled water, to make 1,000 cc.). In order to guard against contamination, and also to lessen the condensation of moisture during the sudden cooling incident to exposure, the plates were poured two days prior to use. The dishes were kept firmly closed, except during exposure, by heavy rubber bands. Exposures were made, generally for a thirty-second period, by extending the dish at arm's length from the cabin window, removing the top and replacing it by hand.

Although the plates were exposed in the disturbed air in the wake of the propeller, it has been demonstrated by Meier and Lindbergh (1935) that the rush of air during the early stages of flight thoroughly removes dust particles from the surfaces of the plane, so that contamination from this source must be regarded as unlikely. This conclusion is supported by the occasional occurrence of a sterile Petri dish, following an exposure of thirty seconds to the air stream, as well as by the data concerning the decrease in organisms at increasing altitudes. Approximately seventy-five plates were exposed in the course of this work. Adequate controls were provided by two plates, carried along at each flight, but unexposed, in which no colonies developed after incubation.

For each flight, records of the ground dry-bulb temperature, wet-bulb temperature (dew point), relative humidity, wind direction, wind velocity, and cloud formations were provided by the Weather Bureau. On the December 6 flight to 10,600 feet, supplementary readings of the air temperature at various altitudes were obtained from a thermometer mounted on the wing strut. For each plate exposed, records of the altitude, the length of the exposure (usually thirty seconds), and the air speed of the plane were taken. From this information, the area of the surface of the Petri dish exposed, and the counts of colonies which developed upon incubation of the plates, quantitative data as to the number of organisms present per cubic foot of air at the various altitudes were secured.

The plates were incubated at room temperature for seventy-two hours, at which time counts were made of the number of bacterial and fungus colonies. Yeasts and actinomycetes were included with the bacteria in these

counts. From each macroscopically distinct type of colony developing on each plate, transfers were made to slants of nutrient agar, and the resulting cultures were used in identification of the various organisms collected.

BACTERIA

Previous investigations, including those of Mischustin (1926), Walker (1935), Proctor (1934, 1935), Rogers and Meier (1936), Proctor and Parker (1938) and Rittenberg (1939), have disclosed that in the upper air bacteria are far more numerous than fungus spores or other organisms. Counts of bacterial colonies were made on all the plates exposed, and a limited number of them, including the plates exposed at the 6,000–10,600 ft. levels on December 6, 4,000–6,000 ft. on January 25, and 2,000–3,500 ft. on February 22 were selected for detailed taxonomic studies.

From these plates, sixty-one isolates, representing twenty-nine distinct species, were identified according to the characteristics given in the fifth

TABLE 1

Bacteria found in the upper air

The figures indicate the number of isolates of each species which were identified

	Dec. 6	Jan. 25	Feb. 22	Total
Achromobacter cystinovorum Barber and Burrows	0	1	0	1
Achromobacter guttatum (Zimmermann) Bergey	0	1	0	1
Achromobacter liquidum (Frankland and Frankland) Bergey	0	0	1	1
Bacillus adhaerens Laubach	0	1	1	2
Bacillus agri Laubach and Rice	0	3	1	4
Bacillus cereus Frankland and Frankland	1	2	0	3
Bacillus fusiformis Gottheil	0	0	1	1
Bacillus megatherium DeBary	2	1	1	4
Bacillus mesentericus Trevisan	0	4	0	4
Bacillus mycoides Flügge	0	0	1	1
Bacillus subtilis Cohn	0	3	0	3
Bacillus ubicuitarius Soriano	0	1	0	1
Flavobacterium devorans (Zimmermann) Bergey	2	1	0	3
Flavobacterium fuscum (Zimmermann) Bergey	0	0	1	1
Flavobacterium lacunatum (Wright) Bergey	0	0	1	1
Flavobacterium sulfureum Bergey	0	2	1	3
Micrococcus aurantiacus (Schröter) Cohn	0	0	1	1
Micrococcus candicans Flugge	1	0	0	1
Micrococcus conglomeratus Migula	1	0	0	1
Micrococcus corallinus Cantani	0	1	0	1
Micrococcus flavus Lehmann and Neumann	0	0	3	3
Micrococcus freudenreichii Guillebeau	4	1	3	8
Micrococcus luteus (Schröter) Cohn	0	0	1	1
Micrococcus perflavus Bergey	0	0	1	1
Micrococcus roseus Frankland and Frankland	1	0	0	1
Micrococcus subcitreus Migula	1	1	0	2
Pseudomonas striata Chester	0	1	0	1
Sarcina flava DeBary	2	1	0	3
Serratia plymouthensis (Migula) Bergey	1	0	2	3

edition of Bergey's *Manual of Determinative Bacteriology*. The species found, and the number of cultures of each which were identified, is presented in table 1.

Spore-forming rods, of the genus Bacillus, comprise 37.7 per cent of the cultures, while 24.6 per cent are non-spore-forming rods, and 37.7 per cent are cocci. A comparison may be made with the figures 52.2 per cent, 20.0 per cent and 27.8 per cent respectively, cited by Proctor (1934), showing that fewer spore-formers and more cocci occurred among the present collections.

All of the spore-forming rods collected proved to be Gram positive. Likewise all of the cocci (with the exception of two Gram variable organisms) were Gram-positive. Both Gram-negative and Gram-positive non-spore-forming rods were obtained, however, the former group being the more numerous.

It is of more than passing interest to compare the present list of bacteria with the forty-nine species collected by Proctor (1934, 1935) and Proctor and Parker (1938). Eleven species; namely, *Bacillus cereus*, *B. megatherium*, *B. mesentericus*, *B. mycoides*, *B subtilis*, *Micrococcus candidus*, *M. corallinus*, *M. conglomeratus*, *M. flavus*, *M. perflavus*, and *Sarcina flava* are to be found in both lists. The similarities between the two studies are, however, greater than is shown by the number of identical species. Proctor et al. list three species of *Flavobacterium* and seven species of *Achromobacter*. The present list includes four species of *Flavobacterium* and three of *Achromobacter*, but no single species is common to both lists. Proctor found only two genera not isolated at Nashville, namely *Kurthia* and *Staphylococcus*, and the present list has only two genera, *Pseudomonas* and *Serratia*, not found by him. If one makes allowance for the fact that the same genera may be represented by different species, and that many of Proctor's cultures were isolated from altitudes greater than those studied by us, the accordance between the two lists is very close.

The findings of Proctor (1934) and Rittenberg (1939) that aerial bacteria generally are of types commonly found in soil or water, that they are in general unable to ferment the common sugars with formation of gas, and that they are characteristically unable to produce indol is borne out by our studies.

FUNGI

One hundred and twenty isolates, obtained at different altitudes on the various flights, were identified to genus. Except in a few genera, identification to species was difficult or impossible, because of lack of adequate keys and of type cultures for purposes of comparison. The cultures included representatives of one genus of Phycomycetes, one of Ascomycetes, and fourteen genera of the Fungi Imperfecti. Among the latter, most of the

isolates belonged to the families Moniliaceae and Dematiaceae of the Moniliales, the two families being about equally well represented. One genus of the Tuberculariaceae and one of the Phomales were also encountered. The various genera, next to be discussed separately, with the number of cultures studied from the various flights, are listed in table 2.

MUCOR. Two cultures obtained at low altitudes on February 22 were examined by Dr. Victor M. Cutter, Jr., who found that they belong to the section *Micromucor*, and are closely related to *Mucor ramanianus*. Chlamydospores and sporangia, but not zygospores, are produced in culture. Species of *Mucor* and *Rhizopus* have been previously obtained from the upper air by Rogers and Meier (1936) and Tasugi and Kurosawa (1938).

CHAETOMIUM. Two cultures, isolated on December 6 at altitudes of 1,000 and 3,000 feet, were identified as *C. murorum* Corda. The characteristic setosely appendaged perithecia, containing eight-spored asci, are produced abundantly in culture. This genus has previously been found in the aerial flora by Meier, Stevenson and Charles (1933).

ACLADIUM. A single culture, obtained from a plate exposed at 8,000 feet on December 6, was identified as a member of this genus. The conidia are hyaline, globose to ellipsoid, with smooth walls, and are borne in a pleurogenous fashion on simple conidiophores.

ASPERGILLUS. Two species of *Aspergillus* were isolated. On January 25, at an altitude of 3,500 feet, cultures were obtained of a black-spored species of the *A. niger*-group, with minutely spinulose conidia and sterigmata in a single series. This isolate corresponds with the description of *A. luchuensis*.

A. terreus was collected twice, at 5,800 feet on January 25, and again on February 22 at 3,500 feet. It is characterized by yellowish brown conidial heads, bearing both primary and secondary sterigmata.

CEPHALOTHECIUM. Two similar strains of *Cephalothecium* were encountered on January 25 and February 22, both at an altitude of 1,500 feet. The mycelium in culture has a fluffy appearance, and bears capitately groups of two-celled pinkish conidia. The occurrence of this genus in the upper air has been reported by Stakman et al. (1923).

OOSPORA. A single isolate referable to this genus was collected from the 2,200 foot level on February 22.

PENICILLIUM. The only species of *Penicillium* to appear in the present collections was an unidentified form of the group Asymmetrica, obtained on January 25 at an altitude of 2,500 feet.

SCOPULARIOPSIS. At an altitude of 1,600 feet on October 26, a single culture of *Scopulariopsis brevicaulis* (Sacc.) Bain, was obtained. Identification was made by Dr. D. H. Linder. This species, sometimes placed in the genus Penicillium, produces conidia of a cinnamon brown color, with warted walls. It is known to cause infections of the toe-nails and finger-nails in man, and

is perhaps even better known because of its physiological property of breaking down arsenic compounds to liberate arsine.

VERTICILLIUM. Six closely similar isolates of *Verticillium* were collected on October 19, October 26, November 9, and December 6 at altitudes of 1,000–1,500 feet. The mycelium bears numerous lateral whorled conidiophores, each of which bears a single ellipsoid conidium at its tip. The conidia separate so readily from the tips of the conidiophores that it is difficult to find a mature one attached in microscopic preparations. From the evidence at hand, it appears probable that *Verticillium* is almost always present in small quantities in the air over Nashville.

ALTERNARIA. Twenty-seven isolates of *Alternaria* were studied during the course of this work. This genus was collected on all flights except one. Of twenty-one plates exposed on December 6, *Alternaria* was found upon eight, one of which was exposed at an altitude of 7,000 feet. It appears, therefore, that *Alternaria* spores are commonly present in the air in rather large quantities. This finding confirms the experience of Stakman et al. (1923), Meier, Stevenson and Charles (1933), Durham (1937, 1938, 1941), and Tasugi and Kurosawa (1938).

BRACHYSPORIUM. This genus, characterized by two–four celled, dark brown or black phragmosporous conidia, was found only once, at an altitude of 1,000 feet on November 9. It has been reported from the air over Tokyo by Tasugi and Kurosawa (1938).

HELMINTHOSPORIUM. In the experience of many others, including Stakman et al. (1933), Meier, Stevenson and Charles (1933), Durham (1937), and Tasugi and Kurosawa (1938), *Helminthosporium* is of rather common occurrence in the air. Two collections on February 22, at an altitude of 1,500 feet, indicate that the brown, multicellular, elongate spores characteristic of this genus do not appear to be nearly so common near Nashville as elsewhere.

HORMODENDRUM. Twenty-four of the 120 cultures studied belong to the genus *Hormodendrum*. It was isolated on every flight with the exception of the one made on October 26. A culture from one of the earlier flights was identified by Dr. N. F. Conant. Plates exposed on December 6 at altitudes of 10,000 and 10,600 feet contained colonies of *Hormodendrum* but of no other fungi. The large number of isolates obtained, and the consistent collection of this genus in most of the flights indicates that *Hormodendrum* is constantly present in rather large amounts in the air. This result confirms the findings of many other workers, including Stakman et al. (1923), Meier, Stevenson and Charles (1933), Meier and Lindbergh (1935), Proctor and Parker (1938), Tasugi and Kurosawa (1938), Durham (1938), and Rittenberg (1939).

MACROSPORIUM. A species of *Macrosporium* was collected from a low alti-

tude on February 22. This genus has been previously reported from the air by numerous workers, including Brown (1930), Meier, Stevenson and Charles (1933), Meier and Lindbergh (1935), Proctor and Parker (1938) and Tasugi and Kurosawa (1938). It has been reported also from the stratosphere by Rogers and Meier (1936).

FUSARIUM. No less than thirty-five cultures of this genus of the Tuberculariaceae were obtained. *Fusarium* was found on all of the flights made except that on November 9. On February 22, it was collected as high as 3,500 feet, but it appears to be restricted generally to lower altitudes.

Although many of the cultures produce the characteristic four-celled, fusoid, curved conidia in abundance, a considerable number produced no spores whatsoever on nutrient agar. Non-pigment-producing forms were most abundant. Two cultures from the flight of October 19, studied by Dr. C. D. Sherbakoff, were identified by him as *F. reticulatum* Mont. In addition, a few cultures characterized by the production of yellow pigments, and a few producing red pigments were collected.

Although *Fusarium* spores have been previously isolated from the air by Meier, Stevenson and Charles (1933), and Durham (1937, 1941), it would seem that further studies of the aerial dissemination of *Fusarium* spores should be made by plant pathologists, because of the great economic importance of diseases caused by members of this genus.

PLENOZYTHIA. A pycnidium-producing fungus, referable to this genus of the Phomales, was found at an altitude of 6,000 feet, on December 6, and again on February 22 at 3,500 feet. Groups of pycnidia, within which immense numbers of hyaline pycnidiospores are formed, are produced on agar. This genus was found by Rittenberg (1939) in plates exposed on shipboard several hundred miles off the California coast.

From the data assembled in table 2, it is apparent that species of *Alternaria*, *Fusarium*, and *Hormodendrum* make up the greater proportion of the fungi of the air over Nashville, and are practically constantly present. *Verticillium*, also, appears to be constantly present in small amounts. The remaining fungi must be regarded as of sporadic occurrence.

Proctor (1934), Proctor and Parker (1938), and others have found species of *Aspergillus* and *Penicillium* to make up a very large proportion of the fungi isolated from air. The present collections, in which only six of 120 fungus cultures belong to these genera, is in marked contrast to these findings.

It is of interest to compare the present findings with the results of Pennington (1940), who made daily spore counts from slides exposed at the ground level in Nashville. *Hormodendrum*, *Alternaria*, *Spondylocladium*, *Acrothecium*, *Helminthosporium*, and *Fusarium* were the most abundant genera, but smut spores, *Aspergillus terreus*, and other *Aspergilli* were also

obtained. Except for collection of *Spondylocladium*, *Acrothecium*, and smuts, the fungi at the ground level are quite like those in the upper air.

YEASTS

The occurrence of yeasts in the aerial flora has been reported by Brown (1930), Proctor (1934), and Tasugi and Kurosawa (1938). A pink, non-spore-forming species of *Saccharomyces* was found by us on plates exposed at 10,000 feet on December 6, and again at 5,800 feet on January 25.

ACTINOMYCETES

Both Mischustin (1926) and Proctor (1934) have reported that Actinomycetes are represented in the microflora of the air, but have not attempted to identify the species found. *Actinomyces griseolus* was isolated by us from a plate exposed at 4,700 feet altitude on January 25, and at 2,200 feet on February 22. *A. phaeochromogenus* occurred on plates exposed at 2,000 feet on February 22.

OTHER ORGANISMS

Meier and Lindbergh (1935) and van Overeem (1936) collected a number of green algae and diatoms from the air during airplane flights. The latter investigator isolated, from an altitude of 2,000 meters, a "moss protonema, which, transferred to a solid medium, has yielded fair-sized moss plants." In the hope of obtaining algae or other chlorophyll-bearing organ-

TABLE 2

Summary of the various types of fungi collected and their relative abundance on different dates

	Oct. 19	Oct. 26	Nov. 9	Dec. 6	Jan. 25	Feb. 22	Total
Acladium				1			1
Alternaria	3		2	13	6	3	27
Aspergillus					3	1	4
Brachysporium			2				2
Cephalothecium					1	1	2
Chaetomium				2			2
Fusarium	7	11		5	2	10	35
Helminthosporium						2	2
Hormodendrum	3		5	12	2	2	24
Macrosporium						1	1
Mucor						2	2
Oospora						1	1
Penicillium					2		2
Plenozythia				1		1	2
Scopulariopsis		1					1
Verticillium	1	2	2	1			6
Actinomyces					1	2	3
Saccharomyces				1	1		2

isms, plates of a medium composed of a modified Detmer's solution solidified by the addition of 1.5 per cent agar were exposed on February 22 at altitudes ranging from 1,000 to 3,000 feet. These plates were brought into the laboratory, and incubated for a week under condition of moderately low temperature, high humidity, and continuous illumination provided by a 25-Watt bulb, but the results obtained were entirely negative.

ABUNDANCE OF THE VARIOUS TYPES OF ORGANISMS

At the time of exposure of each plate, records were made of altitude, length of the exposure, and speed of the plane. Counts of the number of bacterial and fungus colonies were made after an incubation period of three days, as previously stated. From this information, as a basis together with the area of the surface of the Petri dish (9.6 sq. inches, or 0.067 sq. feet) calculations were made of the number of organisms per cubic foot of air, for each plate exposed.

TABLE 3

The abundance of organisms at different times, in relation to the weather conditions

Date	Temp. F. °	Rel. humidity, %	Wind	Organisms per cubic foot	Bacteria colonies: % of total	Fungus colonies: % of total
Oct. 19	81	45	NNE 5	0.65	61.3	38.7
Oct. 26	74	27	S 12–13	0.95	88.7	11.3
Nov. 9	38	67	W 7	0.20	77.7	22.3
Dec. 6	42	45	NNW 16	0.52[a]	66.2	33.8
Jan. 25	56	37	WSW 8–9	0.27[a]	95.9	4.1
Feb. 22	52	36	WSW 2	0.14[a]	90.1	9.9

[a] Inasmuch as these three flights were made at higher altitudes than the first three, the figures given are for all exposures at 1,000–2,000 feet.

It must be borne in mind that the technique employed imposes certain limitations. The figures refer only to viable organisms capable of growth on the particular medium employed under aerobic conditions. Furthermore, the ground speed of the plane is open to considerable inaccuracy of measurement because wind direction and velocity were not taken into account.

The calculations from all seventy-six plates exposed, regardless of altitude, gave an average of 0.21 organisms per cubic foot of air. The maximum, of 1.19 organisms per cu. ft., was obtained on a plate exposed at 1,500 feet on October 26, while none was obtained on a plate exposed for thirty seconds at 6,000 feet on December 6.

The data concerning the abundance of organisms at various times are too voluminous for detailed presentation, but a condensed summary is included in table 3.

The data in the above table indicate fluctuations in the populations of microorganisms at the 1,000–2,000 foot levels varying from 0.14 to 0.95

organisms per cubic foot. It has been impossible to correlate these findings with the existing weather conditions. All flights were made on days in which no rain had fallen for several days previously, so that decreases in the populations due to this factor may be ruled out. The high counts obtained on October 26 are probably causally related to the combination of very dry air and a high wind, and it appears significant that the lowest counts were obtained on February 22, when the wind velocity was least. It is admitted, however, that the atmospheric conditions at a given altitude may be very different from those encountered at the ground level, and that a much larger number of observations would be required to yield results of decisive value.

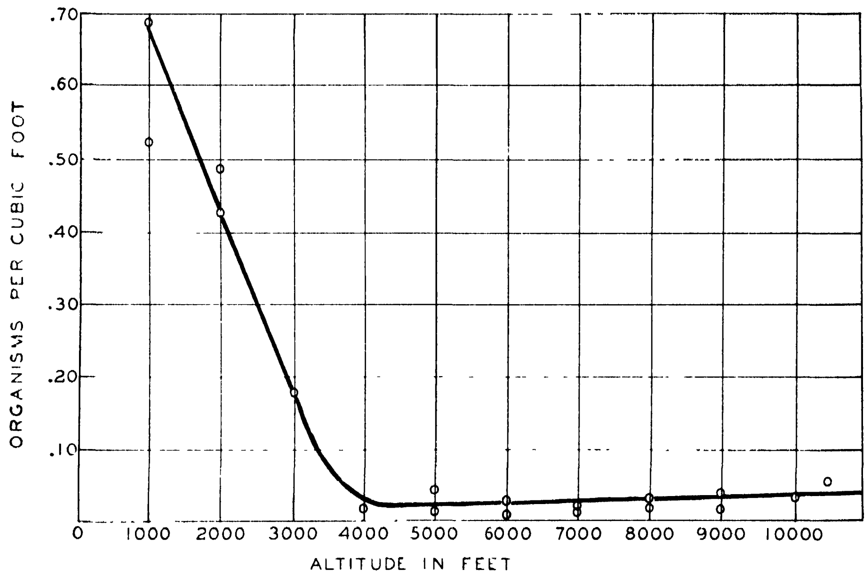


FIG. 1. The distribution of organisms at various altitudes over Nashville, Tenn., on Dec. 6, 1941.

The general decrease in concentration of organisms with increasing altitude is shown in the accompanying graph (fig. 1) based upon data gathered on the flight to 10,600 feet elevation. The entire series of exposures, on this particular flight was made at temperatures below freezing, with a minimum of 22° F. being recorded at 5,000 feet. The concentration of organisms fell sharply between 1,000 and 4,000 feet, above which altitude a small but rather constant population was found.

Proctor (1934) has presented evidence for the existence of "biological strata" in which microorganisms may be present in higher quantities than in the air above or that below the given level, due to vertically localized weather conditions and air movements. This finding is borne out by results obtained on January 25, in which much higher counts were obtained at the

3,000–4,000 foot levels than at either 2,000 or 5,000 feet (fig. 2). The factors responsible for this condition are as yet little understood, and must await further experimentation.

According to Proctor (1934), "the biological population of the upper air is probably an ever-changing one, never constant either in type or in distribution, due to the many factors which may interact at the same time."

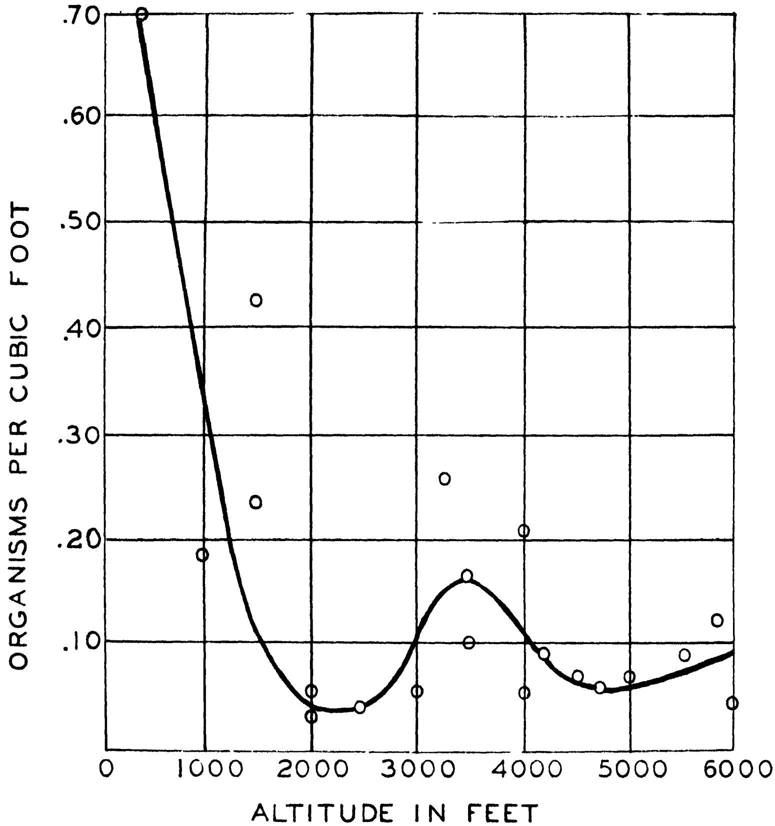


FIG. 2. The distribution of organisms at various altitudes over Nashville, Tenn., on Jan. 25, 1942. Note the higher counts between 3,000 and 4,000 feet.

In the present experiments bacteria were always more abundant than fungus spores, and composed from 61.3 to 95.9 per cent of the total microflora of the air. The proportion of fungi varies from day to day between 4.1 and 38.7 per cent of the total. Yeasts and actinomycetes were never abundant, and together they make up somewhat less than 1 per cent of the microorganisms of the air.

SUMMARY

Studies of the microbiology of the air over Nashville, Tennessee, were

made by exposing Petri dishes containing nutrient agar from airplanes. Twenty-nine different species of bacteria, including species of *Achromobacter*, *Bacillus*, *Flavobacterium*, *Micrococcus*, *Pseudomonas*, *Sarcina*, and *Serratia*, were identified from the plates exposed. Spore-forming rods and cocci were about equally abundant, with non-spore-forming rods being present in lesser concentrations.

Sixteen genera of fungi, including species of *Mucor*, *Chaetomium*, *Acladium*, *Aspergillus*, *Cephalothecium*, *Oospora*, *Penicillium*, *Scopulariopsis*, *Verticillium*, *Alternaria*, *Brachysporium*, *Helminthosporium*, *Hormodendrum*, *Macrosporium*, *Fusarium*, and *Plenozythia* were found. *Alternaria*, *Hormodendrum*, and *Fusarium* species appear to be most abundant and to be consistently present.

Quantitative data were secured indicating an overall average of 0.21 organisms per cubic foot of air. This concentration of organisms is subject to wide variation, induced by a number of factors.

Bacteria were the most abundant group of microorganisms occurring in the upper air, composing 61.3 to 95.9 per cent of the total. The proportion of fungi varied from 4 1 to 38.7 per cent of the total number of microorganisms. Yeasts and actinomycetes were also present in small quantities.

The writer acknowledges with thanks the assistance rendered by Dr. F. A. Wolf, who has identified the bacteria collected during this work, and has criticized the manuscript. He is also deeply appreciative of the courteous cooperation of Dr. N. F Conant, Dr. V. M. Cutter, Jr., Dr. D. H. Linder, and Dr. C. D. Sherbakoff in identifying certain of the fungus cultures. Assistance in the laboratory work involved in this study was provided by a grant-in-aid from the Graduate School of Vanderbilt University.

DEPARTMENT OF BIOLOGY, VANDERBILT UNIVERSITY
NASHVILLE, TENNESSEE

Literature Cited

Bisby, G. R. 1935. Are living spores to be found over the ocean? Mycologia **27:** 84-85.

Brown, J. G. 1930. Living micro-organisms in the air of the arid southwest. Science **72:** 322 323.

Chatterjee, G. 1931. A note on an apparatus for catching spores from the upper air. Indian Jour. Agr. Sci. **1:** 306–308.

Committee on Apparatus in Aerobiology, National Research Council, 1941. Techniques for appraising air-borne populations of micro-organisms, pollen, and insects. Phytopathology **31:** 201 225.

Craigie, J. H. & Popp, W. 1928. Rust epidemiology. Canad. Dep. Agr. Rep. Dom. Bot. **1927:** 47 54.

Durham, O. C. 1937. Incidence of air-borne fungus spores. I. *Alternaria*. Jour. Allergy **8:** 480 490.

————. 1938a. Incidence of air-borne fungus spores. II. *Hormodendrum*, *Alternaria*, and rust spores. Jour. Allergy **10:** 40–49.

———— ——. 1938b. An unusual shower of fungus spores. Jour. Am. Med. Assoc. **111**: 24–25.

———— ——. 1941. Methods in aerobiology. Jour. Aviation Med. **12**: 153–162.

Hubert, Kurt. 1932. Beobachtungen über die Verbreitung des Gelbrostes bei künstlichen Feldinfektionen. Fortschr. Landw. **7**: 195–198.

Jacobs, W. C. 1939. A discussion of the physical factors governing the distribution of microorganisms in the atmosphere. Jour. Marine Res. **2**: 218–224.

MacQuiddy, E. L. 1935. Air studies at higher altitudes. Jour. Allergy **6**: 123–127.

Meier, F. C. 1936a. Collecting micro-organisms from winds above the Caribbean Sea. [abstract] Phytopath. **26**: 102.

———— ——. 1936b. Effects of conditions in the stratosphere on spores of fungi. Nat. Geog. Soc. Contrib. Tech. Papers, Stratosphere Series, 2: 152–153.

Meier, F. C. & Lindbergh, C. A. 1935. Collecting micro-organisms from the Arctic atmosphere. Sci. Monthly **40**: 5–20.

Meier, F. C., Stevenson, J. A. & Charles, V. K. 1933. Spores in the upper air. [abstract] Phytopathology **23**: 23.

Mischustin, E. 1926. Zur Untersuchung der Mikroflora der höheren Luftschichten. Centralbl. Bakt. II **67**: 347–351.

Overeem, M. A. Van. 1936. A sampling-apparatus for aeroplankton. Proc. Kon. Akad. Wetensch. Amsterdam **39**: 981–990.

Pennington, E. S. 1940. A study of the incidence of air-borne molds and of skin sensitivity to molds. South. Med. Jour. **33**: 931–939.

Peturson, B. 1931. Slide exposures by aeroplane. Canada Dep. Agr. Rep. Dom. Bot. **1931**: 44–45.

Proctor, B. E. 1934. The microbiology of the upper air. I. Proc. Am. Acad. **69**: 315–340.

———— ——. 1935. The microbiology of the upper air. II. Jour. Bact. **30**: 363–375.

Proctor, B. E. & Parker, B. W. 1938. Microbiology of the upper air. III An improved apparatus and technique for upper air investigations. Jour. Bact. **36**: 175–181.

Rittenberg, S. C. 1939. Investigations of the microbiology of marine air. Jour. Marine Res. **2**: 208–217.

Rogers, L. A. & Meier, F. C. 1936. The collection of micro-organisms from the atmosphere above 36,000 ft. altitude. Nat. Geog. Soc. Contrib. Tech. Papers, Stratosphere Series, 2: 146–151.

Stevens, A. W. 1936. The scientific results of the world-record stratosphere flight. Nat. Geogr. **69**: 693–712.

Stakman, E. C., Henry, A. W., Curran, G. C. & Christopher, W. N. 1923. Spores in the upper air. Jour. Agr. Res. **24**: 599–606.

Tasugi, H. & Kurosawa, E. 1938. Fungi in the air. Ann. Phytopath. Soc. Japan **8**: 35–42.

Walker, George. 1935. Bacterial content of the air at high altitudes. Science **82**: 442–443.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 15–25 JANUARY, 1943

THE STRUCTURE AND DEVELOPMENT OF THE SHOOT APEX OF EPHEDRA ALTISSIMA DESF.

ERNEST M. GIFFORD

INTRODUCTION

Although the structure of the shoot apex of *Ephedra altissima* has been previously studied (Schmitz 1874; Groom 1885; Koch 1891), methods of modern micro-technique permit a more precise interpretation of the anatomical features of shoot apices. Recent work (Korody 1937; Foster 1938, 1939, 1940, 1941; Johnson 1939; Cross 1939, 1941, 1942) shows a definite trend in the complexity of the apices of gymnosperms from the seemingly primitive types of apices of the Cycadaceae to the more advanced type of the Taxodiaceae Cross (1939) has shown the apex of *Taxodium* to approach the structural condition characteristic of the angiosperms. There is, however, a definite gap between the two which might be suspected to be bridged by the apex-type or types of the Gnetales. The present study shows that *Ephedra altissima* represents such an intergrading form.

MATERIALS AND METHODS

Apices were obtained from a single plant growing on the campus of the University of California and from plants growing on the Anson S. Blake estate in Berkeley, California. Buds were collected at several intervals between January, 1941, and March, 1941, and in January, 1942. The apices were killed and fixed in three fixatives primarily, *viz.:* (1) Zirkle's basic fixative ($CuCrO_7$, 2.5 g; CuO, 0.05 g; $CuSO_4$, 1.0 g.; H_2O, 100 cc.). (2) Corrosive sublimate, 3.0 g.; butyric acid, 3 cc.; 70% alcohol, 100 cc. (3) Chromic acid (0.5 g.: H_2O, 100 cc.)—neutral formalin (21 cc. commercial; H_2O, 100 cc.); mix equal parts when using. The latter fixative gave the best results. The material was dehydrated, cleared in xylene, and embedded in paraffin according to the method outlined by Ball (1941). Serial longitudinal and transverse sections were cut from 5–8 µ in thickness, stained with tannic acid-iron chloride, and counterstained with safranin (Foster 1934). Drawings were made with a 7.5 × ocular and a 54 × oil-immersion objective.

GENERAL FEATURES OF THE SHOOT SYSTEM

Two types of shoots exist in *Ephedra altissima:* (1) a large type which constitutes most of the shoot system, and (2) a smaller, shorter-lived deciduous type which develops from the nodes of the larger shoots. At each node of the first and more vigorous type, there are three leaves in whose axils the second type of shoot arises. The latter possesses decussate phyllotaxis.

The first indications of growth in the spring appear in the large type of shoot, whose rapid growth is accompanied by the development of the axillary, small shoots.

The large or permanent shoots ultimately cease growth but during the growth period numerous axillary permanent shoots develop at older nodes. The present paper does not deal with the origin of these shoots. Possibly the initiation of these shoots is similar to that of the "pseudo-endogenous" buds of *Taxodium* described by Cross (1939). In the present work only the structure of the apices of the two types of shoots are considered.

In the present investigation it has been found that the average diameter of the shoot apex of 40 vigorous permanent shoots is 180 μ while the height is 80 μ. The apex of the smaller shoot possessing decussate phyllotaxis has an average diameter (30 apices measured) of about 110 μ while 75 μ is common for height.

REVIEW OF LITERATURE

After the formulation of the concept of "apical cell" by Nägeli (1878) many subsequent workers attempted to find in all groups of plants such an apical cell from which all subsequent tissues could be traced. Nägeli was rightfully impressed with the regularity and sequence of cell divisions in the apical cell of Thallophytes and certain Bryophytes and thought that no fundamental difference would be found in the organization of apical tissues in both lower and higher groups of plants.

In attempting to prove the doctrine of Nägeli, Dingler (1882, 1886) stated that it was possible in *Ephedra monostachya* (1882) to observe an apical cell (*Scheitelzelle*), which was prismatic or tetrahedral in form. Korschelt (1884) using *E. vulgaris* agreed with Dingler that an apical cell occurred in this genus as well as in other gymnosperms. Schwendener (1879, 1885) concluded from his studies that the shoot apex of certain gymnosperms is crowned by a group of four juxtaposed apical initials. However, the apical meristem of *Ephedra monostachya* did not have the tetrad of apical cells but possessed an irregular group of initials. As late as 1890, Douliot emphasized his firm opinion that "apical-cell segments" exist in gymnosperms and illustrated his belief with schematic diagrams and elaborate drawings of the cell net.

After the announcement of the histogen theory by Hanstein in 1868, many workers labored to disprove the contentions of the champions of the apical cell theory and to show the universality of histogens. Karsten (see Koch 1891) adopted the histogen theory and maintained that histogens were present in *E. altissima*. According to Schmitz (1874), however, the dermatogen of *E. altissima*, though well defined, was occasionally interrupted by periclinal divisions; and the inner tissue exhibited in no way an organization into a definite central plerome and surrounding periblem. In another

species, *E. campylopoda*, Strasburger (1872) stated that a continuous protoderm was usually present but that the separation of periblem and plerome is hardly ever present. This observation was confirmed by Groom (1885) in *E. altissima*. The next important work was by Koch (1891) who described for the apex of *E. altissima* an inner core, forming the pith, and an outer "Hullgewebe," the latter being more meristematic in nature. In confirmation of his own observations Koch (1891) pointed to the work of Sanio (1863) who found, besides the epidermis, in the apex of *E. monostachya* a "pith" composed of a few cells and an outer somewhat thinner-walled tissue. Koch was the first to present a precise and accurate description of the evident cytological zonation in the shoot apex of *Ephedra altissima* and other gymnosperms.

THE SURFACE LAYER

The vigorous apices of both types of shoots are characterized generally by a discrete surface layer which may well be termed the tunica and will be referred to as such in subsequent discussion. Only one exception to this condition has been found and will be considered later. The tissue other than the tunica will be referred to as the corpus (Schmidt 1924).

The usual configuration of the surface layer in the permanent shoots is that of a continuous layer (figs. 1, 3–11), giving rise to the future epidermis. The cells of the tunica often vary in size, structure, and staining qualities; however, in all apices the tunica is uniseriate.

While the above condition is characteristic of the surface layer of the apex, one exception from a series of 40 buds has been found (fig. 2). This figure depicts an apex in which a periclinal division followed by an anticlinal one, has recently taken place in a cell of the tunica. Thus a group of three genetically related cells has been produced. The cell of the tunica immediately to the left of this group has enlarged greatly and may have been on the verge of a periclinal division at the time of fixation. Such a temporary enlargement of a cell of the apex probably lead some of the earlier workers (Dingler 1882; Korschelt 1884; Douliot 1890) to assume and describe the presence of an apical cell. This apex represents the only clear-cut example of such a division, while other seemingly similar cases fail to show such a condition upon critical examination. It is also interesting to note that this bud showed very vigorous growth. This observation agrees with that of Strasburger (1872) who stated that in vigorously growing vegetative apices of *E. campylopoda* the uppermost dermatogen cell may divide transversely (periclinally). The discovery of this example suggests that such divisions may occur from time to time in many vigorous vegetative shoot apices of *E. altissima*. The sub-apical divisions of these cells resulting from the periclinal divisions augment the corpus. The apical and sub-apical cells, indicated by means of nuclei in figure 2, together as a group resemble the apical

initial group of *Ginkgo biloba* described by Foster (1938). Apparently the formation of such a group of apical initials and their derivatives is associated with vigorous growth and may occur during a certain phase in the development of a particular shoot apex.

THE SUB-APICAL REGION OF THE SHOOT APEX

Directly beneath the tunica layer of the apical meristem lies a region that occupies the focus of meristematic activity. This region may be termed the *sub-apical initiation zone*, and the cells composing it, *sub-apical initials* (figs. 1–11). The latter are similar in position and function, but not in size or structure to the "central mother cells" of *Ginkgo* (Foster 1938). The sub-apical initials produce a *central tissue zone* (fig. 3), precursor of the pith, which, in very vigorous shoots, is characterized by highly vacuolate dividing cells having the appearance of a very sluggish "rib meristem" (Schuepp 1926). The cells of the central tissue zone exhibit polarized growth and progressive elongation. The sub-apical initiation zone gives rise also to the cells of the *peripheral zone*. In striking contrast to the vacuolate dividing cells of the pith-forming region the peripheral cells are rich in protoplasm (figs. 4, 5, 7, 8), and stain deeply; cell divisions rather than elongation of the individual cells dominate in this region. Cortex, leaf primordia, and vascular tissue are ultimately produced from the peripheral zone.

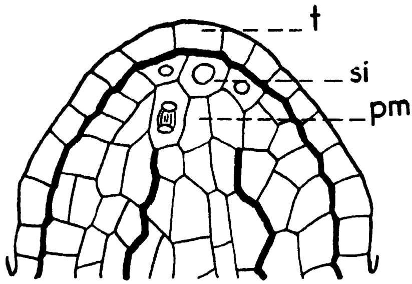
In the majority of the permanent shoot apices studied it was possible to distinguish one tier of sub-apical initials which seemingly were engaged in anticlinal divisions, contributing cells to the peripheral flanks (figs. 3, 4, 5, 7). Directly beneath this group of initials are found the *pith mother cells* (figs. 1, 3, 4, 5, 8). The configuration as described above does not always exist, that is, an upper group of initials dividing only anticlinally. Figure 6 illustrates a periclinal division in a centrally located initial. The same photomicrograph shows how difficult it is to decide which initials give rise to the cells of the peripheral flanks and which contribute to the central zone.

While the configuration as described above is common for many permanent shoot apices, it has been found that the sub-apical initiation zone may consist of two or more tiers of cells engaged primarily in anticlinal divisions (figs. 3, 8).

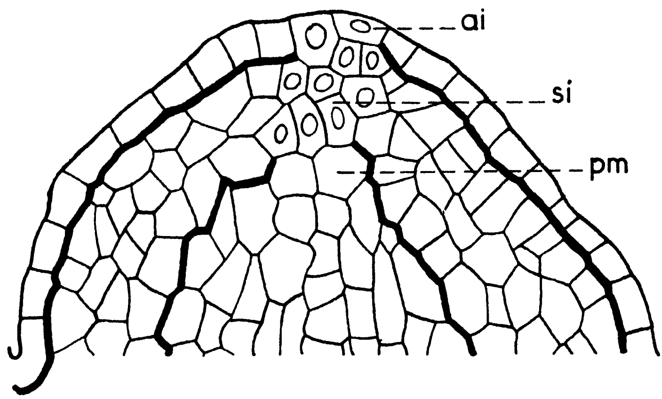
In contrast the apices of the deciduous shoots show no orderly arrangement of the cells of the sub-apical zone. A definite cap of initials in the sub-

Explanation of figures 1–3

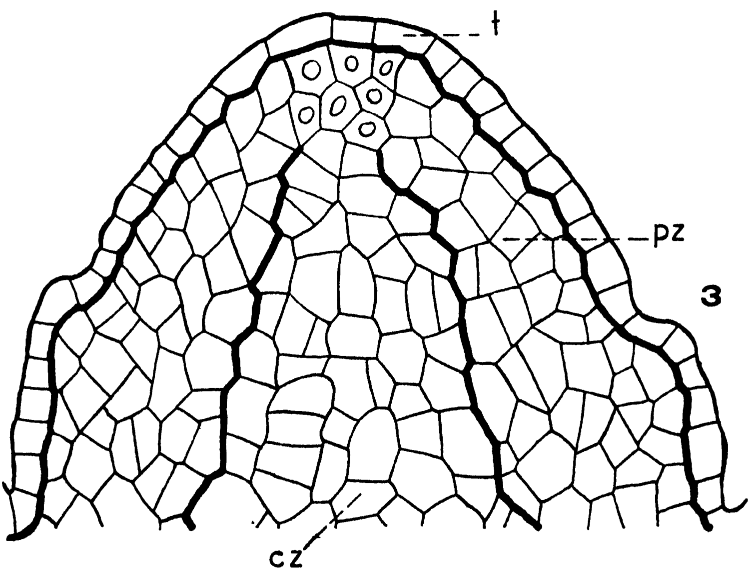
FIG. 1. Median longisection of the shoot apex of an early expanding permanent shoot; *t*, tunica; *si*, sub-apical initials; *pm*, pith mother cells. ×465. FIG. 2. Median longisection of the shoot apex of a vigorous permanent shoot showing evidence of a periclinal division in the tunica. Note also the enlarged cell of the tunica to the left; *ai*, apical initial. ×465. FIG. 3. Median longisection of the shoot apex of a permanent shoot during maximal growth; *pz*, peripheral zone; *t*, tunica; *cz*, central zone. ×465.



1



2



3

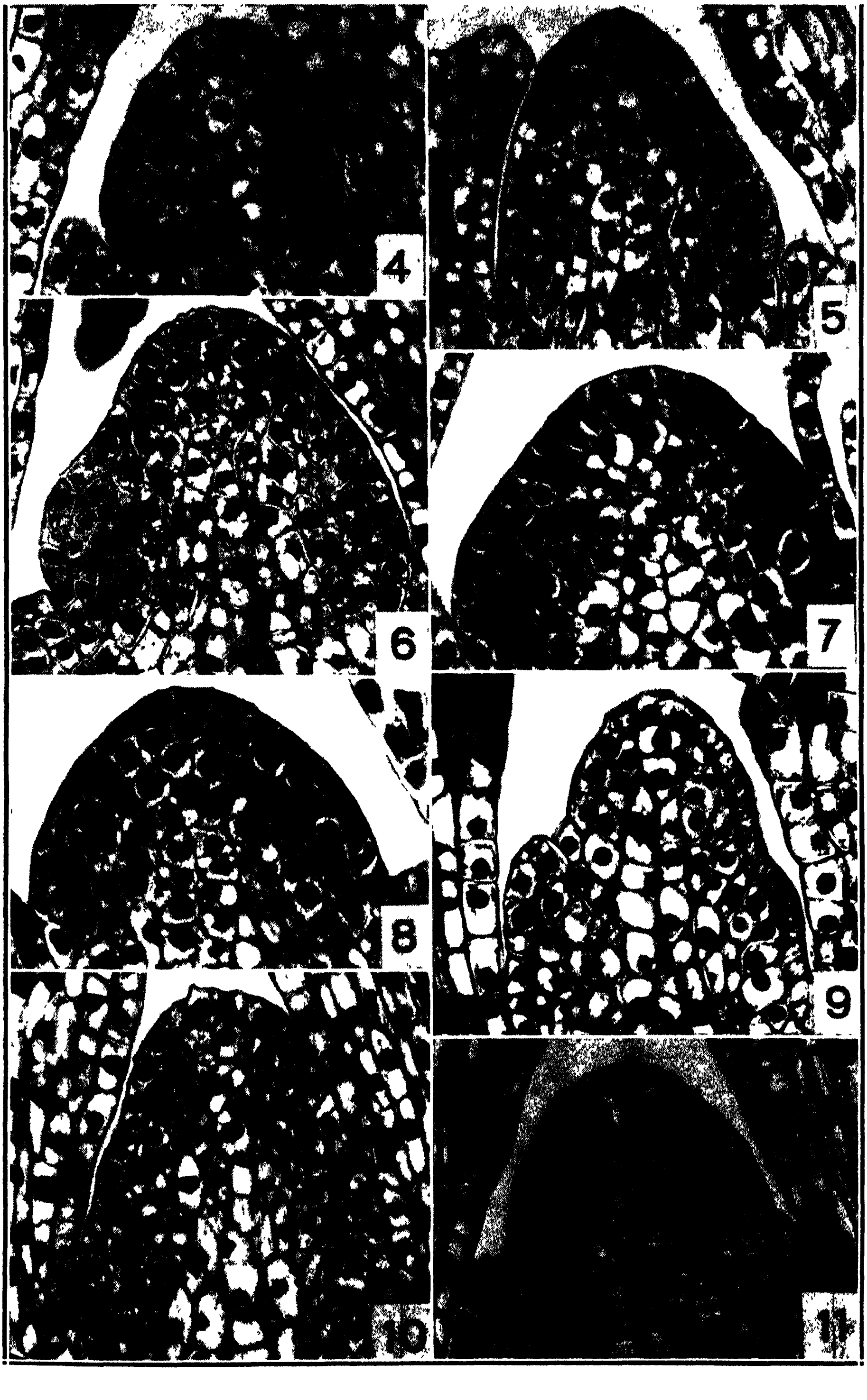
apical zone is hardly ever present. The apices seem to possess a small group of initials which divide periclinally as well as anticlinally. In many apices (figs. 10, 11) the cells of the pith-forming region, or central zone, can be traced up to a cell of the first sub-apical tier of initials directly beneath the tunica.

In some shoots of both types, particularly in vigorous permanent shoots, the cells of the central zone are very regularly arranged in vertical rows. They have the appearance of a true "rib meristem" (figs. 7, 8). Frequently this arrangement is confused by subsequent periclinal and oblique divisions and irregular enlargement of the derivatives of the pith mother cells (figs. 1, 2, 3, 6, 7). This condition is similar to that observed in the shoot apices of *Taxodium distichum* (Cross 1939) and *Cunninghamia lanceolata* (Cross 1941); but in contrast to the clearly defined rib meristem zone in *Ginkgo* and *Dioon* (Foster 1938, 1941). The pith mother cells as well as their derivatives are vacuolate, a feature common to many conifers (Koch 1891, Korody 1937, Cross 1939). Derivatives of the sub-apical initial cells that constitute the meristematic flanks undergo subsequent periclinal and oblique divisions (figs. 1, 2, 3, 5, 7, 8) as well as anticlinal divisions, and no clear stratification as observed in the tunica can be found. These divisions enlarge this zone considerably at the level of a newly forming leaf primordium (figs. 3, 6, 7).

In summary, it appears that the sub-apical region of the shoot apices of *Ephedra altissima* consist in general of three zones characterized by size of cells, structural and staining qualities, and type of division that predominates. Directly beneath the tunica there is a highly embryonic region termed the *initiation zone* from which is produced by anticlinal divisions: (1) *the meristematic flanks*, and by periclinal divisions (2) *the pith mother cells* which give rise in turn to cells constituting the *central zone* or precursor of the pith. The pith mother cells do not maintain their position indefinitely but are ultimately incorporated in the pith; this is followed by a new production of pith mother cells from the tier or tiers of sub-apical initials

Explanation of figures 4–11

FIG. 4. Longisection of shoot apex of an early expanding permanent or large shoot showing a clearly delimited tunica and sub-apical initial group. ×405. FIG. 5. Longisection of shoot apex of a permanent shoot in nearly the same growth phase as fig. 1. ×405. FIG. 6. Longisection of shoot apex of a permanent shoot showing a periclinal division in a sub-apical initial cell directly beneath the tunica. ×405. FIG. 7. Longisection of shoot apex of a permanent shoot in maximal growth. Note the great width of the apex. ×405. FIG. 8. Longisection of a permanent shoot apex in maximal growth illustrating the well defined tunica and stratified nature of the sub-apical initiation zone. ×405. FIG. 9. Longisection of a permanent shoot apex near the cessation of growth. Note the highly vacuolate condition of all the cells. ×405. FIG. 10. Longisection of an apex of the small type of shoot showing the discrete tunica. ×405. FIG. 11. Longisection of the shoot apex of the small type of shoot showing the extent of a row of pith forming cells. ×405.


4
5
6
7
8
9
10
11

directly beneath the tunica. The initiation zone must be regarded as a dynamic and changing entity, governed undoubtedly by volume-surface relations.

SEASONAL VARIATION IN THE STRUCTURE OF THE SHOOT APEX

It was possible on the basis of this investigation of the shoot apex to construct a series showing the changes in structure and configuration of the apical meristem during the course of development of a permanent shoot apex.

Figures 4–9 represent a developmental series beginning with the initiation of growth, through maximal development, and ending with the cessation of growth.

It has been found that in early expanding shoots the apex is relatively small, yet shows discrete tunica and corpus regions (figs. 1, 4, 5). As growth proceeds, the apex becomes more voluminous because of the tendency toward an increase in the width of the central zone or pith-forming region. At a still later period the peripheral zone becomes more stratified (figs. 3, 8) and the central zone assumes in many apices the configuration of a rib meristem. The arrangement of the cells of the sub-apical zone in tiers gives a massive appearance to the apical meristem. It is during this vigorous growth phase that the one exception to the continuous uniseriate tunica was observed. During this period periclinal divisions probably occur in the tunica from time to time in any one particular apex. At the same time the central zone increases decidedly in width (fig. 2) and a rapidity of division of the derivatives of the pith mother cells follows. As growth begins to decline the reverse of the above sequence of events takes place, the configuration becoming as in figure 9. The initiation zone is reduced to a few highly vacuolate cells which sluggishly continue to produce the two zones. The pith becomes narrow and the elongation of its cells dominates over cell division. The cells of the peripheral flanks likewise increase in size and tend to become more vacuolate in nature.

DISCUSSION

The present study does not support the view that *Ephedra altissima* has has an apical cell. In only one of the apices studied was there an indication of a cell that could be interpreted as an apical cell (fig. 2). Possibly the temporary enlargement in depth of a single cell at the apex as is seen in this figure lead Douliot, Dingler and Korschelt to assume the presence of a single apical cell in the terminal meristem of *Ephedra* as well as in the apices of other gymnosperms. The observations of the writer, however, agree in some respects with certain of the earlier investigations. Figure 4 illustrates a condition resembling that described by Karsten (see Koch 1891). According to Karsten the "plerome" ended in one cell and the dermatogen and

"periblem" each consisted of one layer of cells over the apex. That "plerome" and "periblem" may not be sharply defined in *Ephedra altissima*, as emphasized by Schmitz (1874) and Groom (1885), is well illustrated in figs. 2, 6, 11. The type with a central tissue surrounded by a "Hullgewebe" as described by Koch is found in figs. 2, 3, 7, 8.

In recent years certain workers (Korody 1937, Härtel 1938) have attempted to homologize the corpus of the angiospermous apical meristem to the entire shoot apex of certain primitive vascular plants such as *Lycopodium*. A critical examination of this viewpoint has already been undertaken by Foster (1938, 1939b) and Cross (1939, 1941, 1942). The former (1938) came to the conclusion that the apex cannot be looked upon in such a light because such a concept is "based upon too rigid a morphological distinction." In Foster's opinion the tunica and corpus represent "interdependent growth zones" and as such one cannot exist without the other. It is also important to emphasize that while a virtually "stabile" tunica occurs in *Ephedra altissima*, the peripheral zone is only vaguely stratified. "From this standpoint, the evolution of the angiospermous type of shoot apex may have involved an ever increasing emphasis upon surface growth *throughout* the apical and peripheral regions of the meristem." (Foster 1939b). Accepting these two postulates we are led to the concept that through phylogeny there has been an increased stimulus to "surface growth" bringing about the tunica-corpus condition as typified by angiosperms.

Thus a series can be made from the massive condition as exhibited by *Cycas revoluta* (Foster 1939a, 1940) to the more refined types which exhibit to greater or lesser degree the tunica-corpus condition. Some very interesting points of a comparative nature have been brought out by Foster (1941b), who points out that the *Abies venusta* type of apex is common in the conifers; that is, the type characterized by the presence of an outer peripheral zone composed of actively-dividing cells from which arise the epidermis, cortex, leaf primordia, and provascular tissue; and an inner core or central-zone, the precursor of the pith. These zones arise from an ill-defined sub-apical zone which in turn has arisen from derivatives of apical initials. *Araucaria bidwilli* on the other hand has a more regular surface layer. Recently Cross (1939) has found a clearly delimited uniseriate tunica and central corpus in the permanent shoots of *Taxodium distichum*. A similar condition was found by the same author (1941) for the shoot apex of *Cryptomeria japonica*; however, more periclinal divisions were observed in the surface cells of the apex of this plant. In the writer's opinion the condition exhibited by *Ephedra altissima* represents a still further advance in the attainment of the two morphologically independent zones, tunica and corpus.

SUMMARY

The cyto-histological features of the shoot apices of the two types of shoots found in *Ephedra altissima* are described. The apical meristems of all shoots investigated except one are characterized by a uniseriate tunica and a corpus region. One vigorous permanent shoot apex exhibited a periclinal division in the tunica at the summit of the apex.

The sub-apical portion of the apical meristem consists of a sub-apical initiation zone which is the focus of growth and may show a regularity of structure at times. This region gives rise to a central tissue zone and a peripheral tissue zone, each characterized by specific characters. The initiation zone produces "pith mother cells" which divide for a period of time but ultimately are replaced by new pith mother cells from the initiation zone. The peripheral zone increases in width by periclinal divisions as well as anticlinal divisions. Derivatives of this region form the cortex, leaf primordia, and provascular tissue while the epidermis is derived from the tunica.

A comparison of the structure of the shoot apices of *Ephedra altissima* with that of other gymnosperms, leads to a conclusion that the apical meristems of this species represent an advanced condition in this group of plants.

The writer is grateful to Dr. A. S. Foster for his guidance during the research. Thanks are due also to Mr. Louis Erickson for assistance in preparation of the photomicrographs and to Dr. K. Esau who assisted in the preparation of the manuscript.

DEPARTMENT OF BOTANY, UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

Literature Cited

Ball, E. 1941. Microtechnique for the shoot apex. Am. Jour. Bot. **28:** 233–243.

Cross, G. L. 1939. The structure and development of the apical meristem in the shoots of *Taxodium distichum*. Bull. Torrey Club **66:** 431 452.

————. 1941. Some histogenetic features of the shoot of *Cryptomeria japonica*. Am. Jour. Bot. **28:** 573–582.

————. 1942. Structure of the apical meristem and development of the foliage leaves of *Cunninghamia lanceolata*. Am. Jour. Bot. **29:** 288–301.

Dingler, H. 1882. Über das Scheitelwachsthum des Gymnospermen-Stammes.

————. 1886. Zum Scheitelwachsthum der Gymnospermen. Ber. Deuts. Bot. Ges. **4:** 18–36.

Douliot, H. 1890. Recherches sur la croissance terminale de la tige des Phanérogames. Ann. Sci. Nat. VII. **11:** 283–350.

Foster, A. S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. Stain Tech. **9:** 91–92.

————. 1938. Structure and growth of the shoot apex in *Ginkgo biloba*. Bull. Torrey Club **65:** 531–556.

———. 1939a. Structure and growth of the shoot apex of *Cycas revoluta*. Am. Jour. Bot. **26**: 372–385.

———. 1939b. Problems of structure, growth and evolution in the shoot apex of seed plants. Bot. Rev. **5**: 454–470.

———. 1940. Further studies on zonal structure and growth of the shoot apex of *Cycas revoluta*. Am. Jour. Bot. **27**: 487–501.

———. 1941a. Zonal structure of the shoot apex of *Dioon edule*. Am. Jour. Bot. **28**: 557–564.

———. 1941b. Comparative studies on the structure of the shoot apex in seed plants. Bull. Torrey Club **68**: 339–350.

Groom, P. 1885. Ueber den Vegetationspunkt der Phanerogamen. Ber. Deuts. Bot. Ges. **3**: 303–312.

Härtel, K. 1938. Studien an Vegetationspunkten einheimischer *Lycopodien*. Beitr. Biol. Pflanzen **25**: 125–168.

Johnson, M. A. 1939. Structure of the shoot apex of *Zamia*. Bot. Gaz. **101**: 189–203.

Koch, L. 1891. Ueber Bau und Wachsthum der Sprossspitze der Phanerogamen. I. Die Gymnospermen. Jahrb. Wiss. Bot. **22**: 491–680.

Korody, E. 1937. Studien am Spross-Vegetationspunkt von *Abies concolor*, *Picea excelsa* und *Pinus montana*. Beitr. Biol. Pflanzen **25**: 23–59.

Korschelt, P. 1884. Zur Frage uber das Scheitelwachsthum bei den Phanerogamen. Jahr. Wiss Bot. **15**: 642–674.

Nägeli, C. 1878. Ueber das Scheitelwachsthum der Phanerogamen. Bot. Zeit. **36**: 124–126.

Sanio, C. 1863. Vergleichende Untersuchungen uber die Zusammensetzung des Holzkörpers. Bot. Zeit. **21**: 367–375.

Schmidt, A. 1924. Histologische Studien an phanerogamen Vegetationspunkten. Bot. Arch. **8**: 345–404.

Schmitz, K. J. F. 1874. Beobachtungen uber die Entwicklung der Sprossspitze der Phanerogamen. I. Habilitationsschrift, Halle.

Schuepp, O. 1926. Meristeme. In Linsbauer, Handbuch der Pflanzenanatomie. IV.

Schwendener, S. 1879. Ueber Scheitelwachsthum mit mehreren Scheitelzellen. Sitz.-ber. Ges. Naturf. Freunde **1879**: 162–165.

———. 1885. Über Scheitelwachsthum und Blattstellungen. Sitz.-ber. Berlin. Akad. **40**: 921–937.

Strasburger, E. 1872. Die Coniferen und die Gnetaceen.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 26–33 JANUARY, 1943

POLYPLOIDY IN SEDUM PULCHELLUM—I. CYTOGEOGRAPHY[1]

J. T. BALDWIN, JR.

This paper presents the chromosome numbers and geographic occurrence of three polyploid races of *Sedum pulchellum* Michx. as revealed by routine cytological analysis of the species at representative localities in its distributional area.

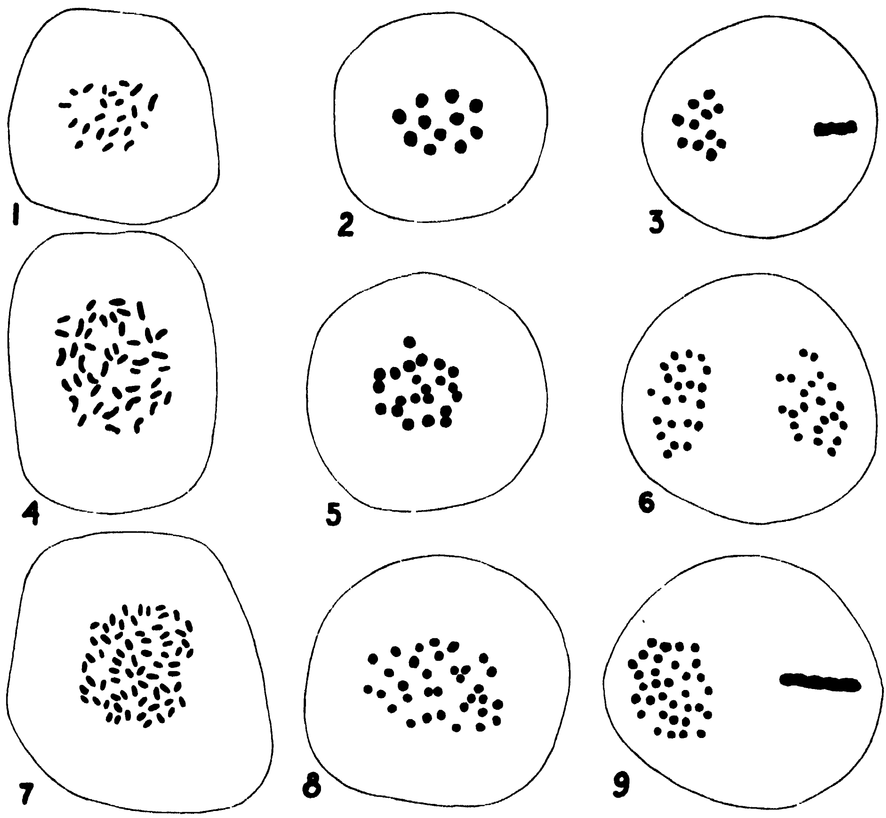
Michaux (1803) described *S. pulchellum* from "circa *Knoxville*," with no mention of the life-length of the plant. From this record Pursh (1814), in spite of having seen neither living nor dead specimens, indicated the species to be perennial. The writer knows the plant throughout its geographic range only as a winter annual, white- or pink-flowered. Wherry (1934), however, reviewed the history of a horticultural perennial of unknown origin that has long been identified with the above species. Nuttall (1818) confused *S. pulchellum* with a perennial later designated *S. nevii* Gray, and under this latter name, since 1858, two perennial sedums of the Appalachian Mountains have been passing (Baldwin 1942a). Torrey and Gray (1840) questioned the pereniality of *S. pulchellum* but accorded it a range which shows that in their concept of the species they incorporated the two perennials of the *S. nevii* group. The reason for the confusion (which continues up to the present) of the identity, range, and life-length of these plants lies in the fact that the juvenile stages of *S. pulchellum*—lasting from fall until spring, when flower-bearing stems are produced, spatulate leaves are lost, and linear, subterete leaves are developed—that these stages strongly resemble the nonflowering plants of the *S. nevii* aggregate.

Plants and/or seed of *S. pulchellum* from forty stations typical of the specific range, seed from four herbarium sheets in the Field Museum, and plants and seed from a huge, self-perpetuating population at The Blandy Experimental Farm in Virginia have supplied material for cytological study (see table 1). Plants and seedlings were grown in the University of Michigan Botanical Gardens. Chromosome counts for the forty-five collections were made from aceto-carmine smears of roots and leaves, and, in a few cases, from Nawaschin-fixed, crystal-violet-stained sections of roots; also, for certain collections of each chromosome-number race, gametic counts were made from aceto-carmine smears of pollen mother-cells.

[1] Paper from the Department of Botany of the University of Michigan, No. 802. Supported by the Faculty Research Fund, Project No. 569.

Publication of the illustrations was assisted by the Lucien M. Underwood Memorial Fund.

A polyploid series was established for the species: twenty-six collections were diploid—$2n = 22$, $n = 11$ (figs. 1–3); sixteen, tetraploid—$2n = 44$, $n = 22$ (figs. 4–6); three, hexaploid—$2n = 66$, $n = 33$ (figs. 7–9). Multivalent associations characteristic of high polyploids with small chromosomes are usually present during meiosis of the tetraploid and hexaploid plants. This doubtless accounts for the existence of atypical plants with $2n$-numbers of



FIGS. 1–9. Chromosomes of *Sedum pulchellum* at mitotic and meiotic (I and II) metaphases. FIGS. 1–3. Diploid: $2n = 22$, $n = 11$. FIGS. 4–6. Tetraploid: $2n = 44$, $n = 22$. FIGS. 7–9. Hexaploid: $2n = 66$, $n = 33$. All, ca. × 1085, from smears: relative sizes of cells are not strictly accurate; cell outlines in figs. 1, 2, and 4 were selected to accompany the metaphases drawn.

64 and 72 as found by the writer in the population at Blandy Farm. At first meiotic metaphase of tetraploid and hexaploid plants the chromosome number is difficult to determine because of the grouped associations—which may often be secondary rather than primary, but at second metaphase counting is comparatively easy. All the plants are highly self-fertile.

The accompanying map (fig. 10) shows the distribution of the species

TABLE 1

Collections of Sedum pulchellum for which chromosome numbers were determined

Source	2n-number	Collector
Missouri		
Polk Co.: Burns	22	*J. A. Steyermark 27232*[a]
Camden Co.: Bannister	22	*J. A. Steyermark 6886*
Cedar Co.: Tilley	22	*J. A. Steyermark 27465*
Moniteau Co.: Jamestown	22	*J. A. Steyermark 24826*
Stone Co.: Galena	22	B & G[b]
Jasper Co.: Joplin	22	B & G
McDonald Co.: Noel	22	B & G
Arkansas		
Lawrence Co.: Imboden	22	B & G
Lawrence Co.: Jesup	22	B & G
Carroll Co.: Busch	22	B & G
Carroll Co.: Eureka Springs	22	B & G
Sharp Co.: Shelbyville	22	B & G
Independence Co.: Batesville	22	B & G
Boone Co.: Francis	22	B & G
Washington Co.: Fayetteville	22	B & G
Benton Co.:	22	B, G & D. M. Moore
Benton Co.:	22	D. M. Moore
Pulaski Co.: Little Rock	22	Delzie Demaree
Oklahoma		
Carter Co.: Ardmore	22	Milton Hopkins
Alabama		
Madison Co.: Monte Sano	22	R. M. Harper
Tennessee		
Knox Co.: Knoxville	22	J. T. Baldwin, Jr.
Jackson Co.: Roaring River	22	B & G
Bedford Co.: Shelbyville	22	B & G
Rutherford Co.: near Bedford County line	22	B & G
Rutherford Co.: Murfreesboro	22	B, S & H[c]
Sumner Co.: near Goodlettsville	44	B, S & H
Cheatham Co.:	44	Jean M. Campbell
Davidson Co.: Nashville	22	B, S & H
Davidson Co.: 14 miles w. Nashville	44	B, S & H
Davidson Co.: 12 miles s. Nashville	44	Jean M. Campbell
Davidson Co.: Nashville	66	B, S & H
Wilson Co.: Lebanon	66	B, S & H
Wilson Co.: Lebanon	66	L. M. Dickerson[d]
Wilson Co.: Cedar of Lebanon State Park	44	B, S & H
Kentucky		
Fayette Co.: Elk Lick Falls	44	Mary E. Wharton
Fayette Co.: Raven Creek	44	B, S & H
Anderson Co.: Tyrone Bridge	44	B, S & H
Woodford Co.: Camp Offut	44	B, S & H
Mercer Co.: Shaker Town	44	B, S & H
Clark Co.: Lower Howard Creek	44	B, S & H
Jessamine Co.: Wilmore	44	H. T. Shacklette
Caldwell Co.: Princeton	44	A. M. Harvill
Simpson Co.:	44	B, S & H
Illinois		
Union Co.: Cobden	44	B & G
Johnson Co.: Sanburn	44	B & G

[a] Seed from herbarium specimen in Field Museum.
[b] J. T. Baldwin, Jr., and Walton C. Gregory.
[c] J. T. Baldwin, Jr., H. T. Shacklette, and A. M. Harvill.
[d] Transplanted to The Blandy Experimental Farm in Virginia about 1930.

and of its races as known to the writer by the collections listed in table 1, by specimens in certain herbaria,[2] and by county-collection records of Palmer and Steyermark (1935) for Missouri. The species occurs from Dade County, Georgia, and Madison County, Alabama, through Tennessee and Kentucky to Union and Johnson counties, Illinois, and, west of the Mississippi River, through much of Missouri and Arkansas into Kansas, Oklahoma and Texas. (Steyermark (1942) has written an extended note on the occurrence of *S. pulchellum* in Missouri.) The present cytological data indicate that only the diploid is found in the western and southern parts of the specific area, that only the tetraploid occurs from northern Tennessee through Kentucky and in Illinois, and that the hexaploid exists only in northern Tennessee in the region of contact between the other two races, being found, for example, on the grounds of Cumberland University at Lebanon, Tennessee. The diploid, and supposedly oldest, race is the most extensively distributed. It is logical to consider that the tetraploid arose from the diploid by chromosome doubling, and, similarly, the hexaploid from an inter-racial triploid. (One would not expect to find an annual established as a triploid: survival of an annual is normally dependent on regular meiosis.) The evidence is that the tetraploid moved northward, and, thus, into the only ecologically suitable territory[3] that was nearby and not already occupied by the species. To attempt, as yet, a statement of the direction of migration of the diploid is hazardous.

S. ternatum, the only other species of *Sedum* for which an intensive cytogeographic study has been made, is, with respect to the conditions just enumerated for *S. pulchellum*, quite different (Baldwin 1942b). It is perennial. Its races can maintain themselves vegetatively. Its diploid race is restricted to a limited area from which the tetraploid has spread radially throughout the specific range. A hexaploid race is known from one station, that being at the southern edge of the range of the species and near the tetraploid. A triploid is known from two places: in West Virginia where both the diploid and tetraploid have been found, and in North Carolina where both these other races might be expected to occur. But *S. ternatum* and *S. pulchellum* have this in common: the tetraploid race, once established, has in each species been more evolutionarily effective than the diploid; the tetraploid in both cases migrated into new territory. The direction of migration, as is generally true, was determined by the whereabouts of accessible and ecologically suitable territory. Tetraploid *S. ternatum* accordingly spread in all directions; tetraploid *S. pulchellum* went north.

---

[2] United States National Herbarium, and herbaria of the Field Museum, the New York Botanical Garden, the University of Arkansas, the University of Tennessee, the University of Kentucky and the University of Michigan. It was a privilege to examine the specimens.

[3] *S. pulchellum* is found "most frequently on limestone, but also . . . on granitic and siliceous rocks" (Palmer and Steyermark 1935).

In the southeastern part of its geographic area *S. pulchellum* extends into the general range of true *S. nevii* Gray, which has 12 somatic, 6 gametic chromosomes (Baldwin 1942a). The *S. nevii* alliance, as stated above, is often confused with *S. pulchellum*. For example: Dr. R. M. Harper sent the writer living specimens of a sedum from Monte Sano, Madison County, Alabama; study showed it to be diploid *S. pulchellum*, but Doctor Harper (letter of February 19, 1941) wrote: "everybody who has passed on my Monte Sano

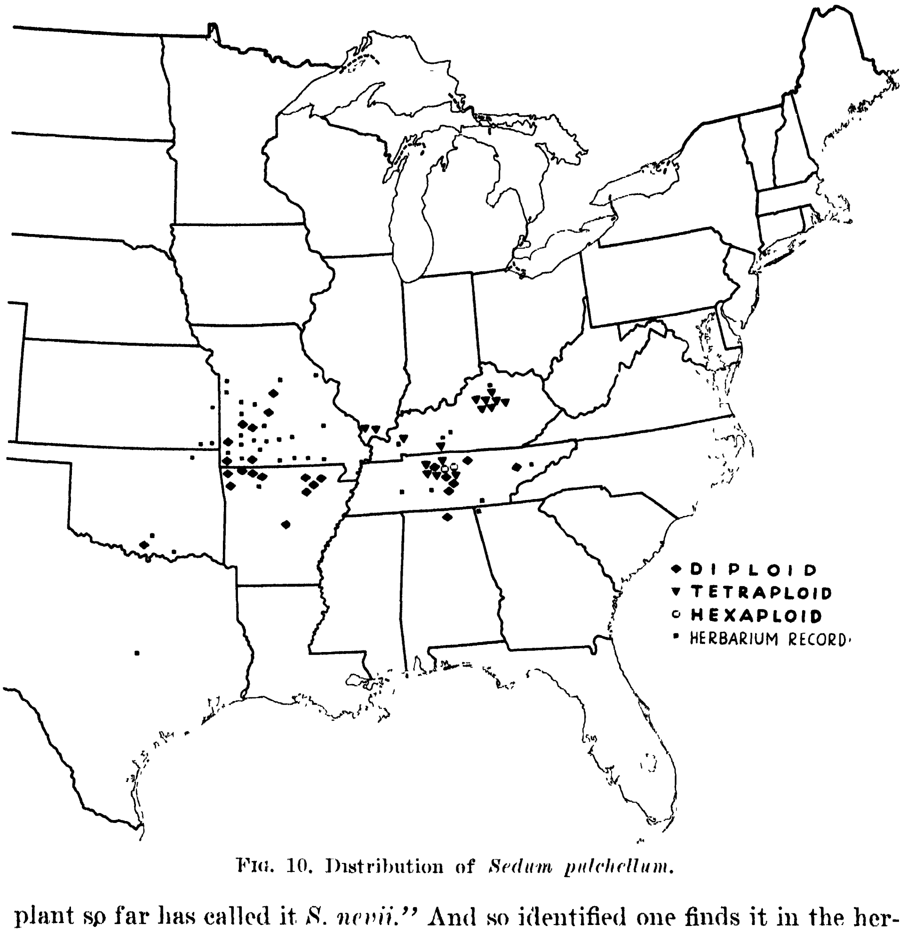


FIG. 10. Distribution of *Sedum pulchellum*.

plant so far has called it *S. nevii*." And so identified one finds it in the herbaria (*R. M. Harper 3780*). In the western part of its area, from Missouri and Kansas to Texas, *S. pulchellum* overlaps the range of *S. nuttallianum* Raf., which has 20 somatic, 10 gametic chromosomes.[4] The dead, fruiting

[4] The writer (1940) reported *S. nuttallianum* from near Georgetown, Texas, to have these numbers. The somatic number has been corroborated by him for a collection made, in company with Doctors Walton C. Gregory and D. M. Moore, in Benton County, Arkansas, during the summer of 1941.

plants of this latter species, a yellow-flowered winter (?) annual, superficially resemble the fruiting stems of *S. pulchellum*. Of course they can be distinguished without difficulty, but they do look somewhat alike, and not infrequently they are confused in herbaria. The species sometimes grow together, for example, in Benton County, Arkansas. The suggestion comes to mind, then, that true *S. nevii* is an expression of a 6-chromosome tendency in evolution and *S. nuttallianum*, as Baldwin (1940) concluded, of a 5-chromosome tendency and that *S. pulchellum* arose as an amphidiploid result of the fusion of these two trends in the development of the genus. The one tendency dominates the characters of the juvenile plant and causes confusion with *S. nevii;* the other dominates the characters of the senescent and dead plant and causes resemblance to *S. nuttallianum*. Accordingly, *S. pulchellum* is to be interpreted as an amphidiploid that has undergone autopolyploidy to produce 44- (amphitetraploid) and 66- (amphihexaploid) chromosome races. This latter plant, with 33 gametic chromosomes, is a high-numbered annual Müntzing (1936) studied statistically chromosome numbers in forty-eight genera that include species with different life lengths; *Sedum* is, obviously, such a genus. He found: "With regard to the annual and perennial series it is striking that *all* species with the haploid numbers ranging from 40 to 105 are perennial."

Under uniform conditions the chromosome-number races of *S. pulchellum* are morphologically different, but nevertheless, since the writer did most of his collecting of the species in the summer, when the plants were dead, he does not know whether or not the races can always be distinguished under field conditions. Judging by cytogeographic evidence alone, one would say that Michaux used the diploid as type material (from Knoxville) for this species and that John K. Small used the same race as type material (from Rising Fawn, Dade County, Georgia) for *S. vigilimontis*. This latter plant, as pointed out by Wherry (1935), is clearly referable to *S. pulchellum*. Fröderström (1935), in his monograph on the genus, recognized Small's species, with the qualification, however, that it is "perhaps but a local variety" of *S. pulchellum*. The late Doctor Jennison, on an herbarium sheet of *S. pulchellum* at the University of Tennessee (*H. M. Jennison 198*, Knoxville city limits, May 28, 1938), wrote: "approaching *S. vigilimontis* Small—the which I do not think is a good species—but only a variety." The writer found plants at this Knoxville station, which must be near the type locality for *S. pulchellum*, to be diploid. The judgment that Small's plant also belongs to the diploid race may be tested by measurement of the type and also by determination of the chromosome number of plants at Rising Fawn, Georgia. Torrey and Gray (1840) state that Nuttall gave a manuscript name, *S. linifolium*, to a form of *S. pulchellum* in Arkansas. Again, on cytogeographic data, one considers that the plant in question was probably diploid.

SUMMARY

Forty-five collections of *S. pulchellum,* from representative places in the specific area, were examined cytologically: twenty-six were diploid—$2n = 22$, $n = 11$; sixteen, tetraploid—$2n = 44$, $n = 22$; three, hexaploid—$2n = 66$, $n = 33$. Multivalent associations occur at meiosis in tetraploid and hexaploid plants. Some deviants from the $2n$-number of 66 were found.

The species is distributed from Missouri to Texas and from southern Illinois through Kentucky and Tennessee to Alabama and Georgia. The diploid is found west of the Mississippi River and in the southern part of the range. The tetraploid has moved from northern Tennessee into Kentucky and Illinois. The hexaploid is found in Tennessee where the diploid and tetraploid races meet. The cytogeographic situation in this species is quite different from that in *S. nevii.* The two species are alike, however, in that the tetraploid, once established, in each species has been more effective evolutionarily than the diploid: the tetraploid in both cases migrated into new territory.

S. pulchellum possibly arose as the amphidiploid result of the fusion of a 6-chromosome tendency, now exemplified by true *S. nevii,* with a 5-chromosome tendency, now exemplified by *S. nuttallianum.* This explanation accounts for the marked similarity—resulting in frequent taxonomic confusion—of the juvenile plants of *S. pulchellum* to nonflowering plants of *S. nevii;* it also explains the resemblance of the matured stages of *S. pulchellum* and *S. nuttallianum,* an annual within the area of *S. pulchellum,* which is likewise annual. Accordingly, *S. pulchellum* is to be interpreted as an amphidiploid that has undergone autopolyploidy.

The three chromosome-number races differ morphologically, but the cytogeographic data indicate that only the diploid has been used—by Michaux, Nuttall, and Small—as a basis for nomenclatorial designation of wild plants of this species.

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

Literature Cited

Baldwin, J. T. Jr. 1940. Cytophyletic analysis of certain annual and biennial Crassulaceae. Madroño **5:** 184–192.

————. 1942a. Cytological basis for specific segregation in the *Sedum Nevii* complex. Rhodora **44:** 10–13.

————. 1942b. Polyploidy in *Sedum ternatum* Michx. II. Cytogeography. Am. Jour. Bot. **29:** 283–286.

Fröderström, H. 1935. The genus *Sedum* L. Pt. IV. Acta Horti Gothob. **10** (Append.): 1–262.

Michaux, A. 1803. Flora Boreali-Americana I. Parisiis & Argentorati, apud fratres Levrault.

Müntzing, A. 1936. The evolutionary significance of autopolyploidy. Hereditas **21:** 263–378.

Nuttall, T. 1818. Genera of North American Plants I. Philadelphia, D. Heartt.

Palmer, E. J. & Steyermark, J. A. 1935. An annotated catalogue of the flowering plants of Missouri. Ann. Mo. Bot. Gard. **22:** 375–758.

Pursh, F. 1814. Flora Americae Septentrionalis I. London, White, Cochrane, & Company.

Steyermark, J. A. 1942. Rediscovering *Sedum pulchellum* at its northeastern limit. Rhodora **44:** 73–76.

Torrey, J. & Gray, A. 1840. Flora of North America. I. New York, Wiley & Putnam.

Wherry, E. T. 1934. The sedums of the eastern United States. Gard. Chron. Am. **38:** 264–266.

———————. 1935. The ranges of our eastern parnassias and sedums. Bartonia No. 17: 17–20.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 34–41 JANUARY, 1943

PLANT SUCCESSION ON ABANDONED FIELDS IN THE CENTRAL WISCONSIN SAND PLAIN AREA[1]

JOHN W. THOMSON, JR.

Juneau County, Wisconsin, is in the part of the central sand plain area which is the bed of Glacial Lake Wisconsin. Here the residual soil of the underlying Cambrian sandstone has been reworked by water to form extensive areas of the Plainfield sandy soil series. In the southeastern part of the county there are large areas of the Boone series of sandy soils which are residual from the Cambrian sandstone but have not been reworked. These soils were much cultivated in Juneau County after settlement, which began in the eighteen-fifties, but their low fertility and their aridity have caused their abandonment in this century. As part of a study of the prairie flora in the central sand plain of Wisconsin, the succession of plants on some of these abandoned fields was observed in Juneau County.

Funds making possible the field work for this study were supplied by the Alumni Research Foundation of the University of Wisconsin. The studies on the abandoned fields were begun during the summer of 1936 by Arthur Oehmcke and the writer and continued in 1937 and 1938 by the writer. Grateful acknowledgment is made to Professor N. C. Fassett of the University of Wisconsin for constant help and suggestions during the progress of this study. I am indebted to my wife, Olive S. Thomson, for assistance in the field and in the preparation of this paper. The generous hospitality of Mr. and Mrs. F. N. Hamerstrom, Jr., made available their home as a center of operations while the field work was in progress.

Information upon the dates of abandonment was supplied mainly by Mr. Leo Laski of Necedah and Mr. Knute Olsen of the Olsen store at Mather. Little information upon the date of last cultivation could be obtained from people living near abandoned fields. Their reluctance may in part be ascribed to the habit of some people in central Wisconsin of farming county land. When definitely dated fields were located which were on ground that was not too low and wet for the study of prairie plants, they were examined during the three successive years. A total of thirteen separate fields were observed during this period. The detailed data are not presented in this paper owing to the exigence of space but may be obtained by consulting the writer's thesis submitted to the University of Wisconsin under the title of "Dynamics of some prairie plants in central Wisconsin." The observations of changes within an individual field were checked against fields of varying

[1] Part of a thesis submitted in partial fulfilment of the requirements for the degree of Ph.D. at the University of Wisconsin, 1939.

ages and the result expressed in the chart, figure 1. On this chart the vertical lines represent the observed comparative abundance of the species; and the dotted lines represent the probable curve of frequency of each species.

DISCUSSION OF THE SUCCESSION ON ABANDONED FIELDS

Field work on the abandoned fields in 1937 and 1938 substantiated the observations made in 1936,[2] although many of the fields had again been put under cultivation and observation on them terminated. The rapid succession or changes in the flora during the first few years is very marked and later changes occur but slowly. While these observations were made on land which had been under cultivation for several years and then abandoned, Mr. F. N. Hamerstrom, Jr., informed the writer that the succession which he had observed on plots which were plowed and then allowed to lie fallow with neither cultivation nor manuring, does not agree in its details with the observations noted here. He suggests that the early dominance of ragweed which we observed may be due to the manuring of cultivated fields. In support of this suggestion is an observation made by Mr. Wallace Grange on his property near Babcock, Wood County, in 1938. Here a ditch bank containing much organic matter in the form of peat was burned over and in the burned area arose a dense stand of *Ambrosia artemisiifolia*. Possibly the early dominance of this ragweed in the cultivated fields is dependent upon the presence of considerable organic matter.

The flora which becomes established in any given field will vary, depending on a number of factors including the ability of the plants to produce seed and to secure dispersion of the seed, the nearness of the field to a source of seed and the ecological condition of the field. The occurrence of some of the more conservative prairie plants such as *Desmodium illinoense* on some of the fields is dependent on the proximity of a prairie relic which provided a source of seed. The other plants involved in the succession are dependent on the same set of factors. While individual fields will thus vary somewhat in the plants which are established upon them, the discussion which follows embodies the generalized story of the succession.

In the fields which have been abandoned for but one year, the flora is much the same as during cultivation. There is an abundance of ragweed (*Ambrosia artemisifolia*) and sandbur (*Cenchrus pauciflorus*). Canada Fleabane (*Erigeron canadensis*) is often very common. Of lesser importance is a large group of American weeds of southern distribution. These include *Mollugo verticillata, Leptoloma cognatum, Lepidium apetalum, Oenothera rhombipetala, Oenothera biennis, Panicum albemarlense*, and *Helianthus occidentalis*. A few European weeds may also become established, including

[2] **Thomson, J. W., Jr.** 1937. Dynamics of some prairie plants in Juneau County, Wisconsin. Unpublished thesis for the degree of M.A., Univ. Wis.

Setaria lutescens, Euphorbia maculata, Polygonum convolvulus, and *Rumex acetosella.* Individual plants of a few prairie species may enter the fields during the first year. Among those observed are *Euphorbia corollata,* which at times may even be common, *Andropogon furcatus,* and *Andropogon*

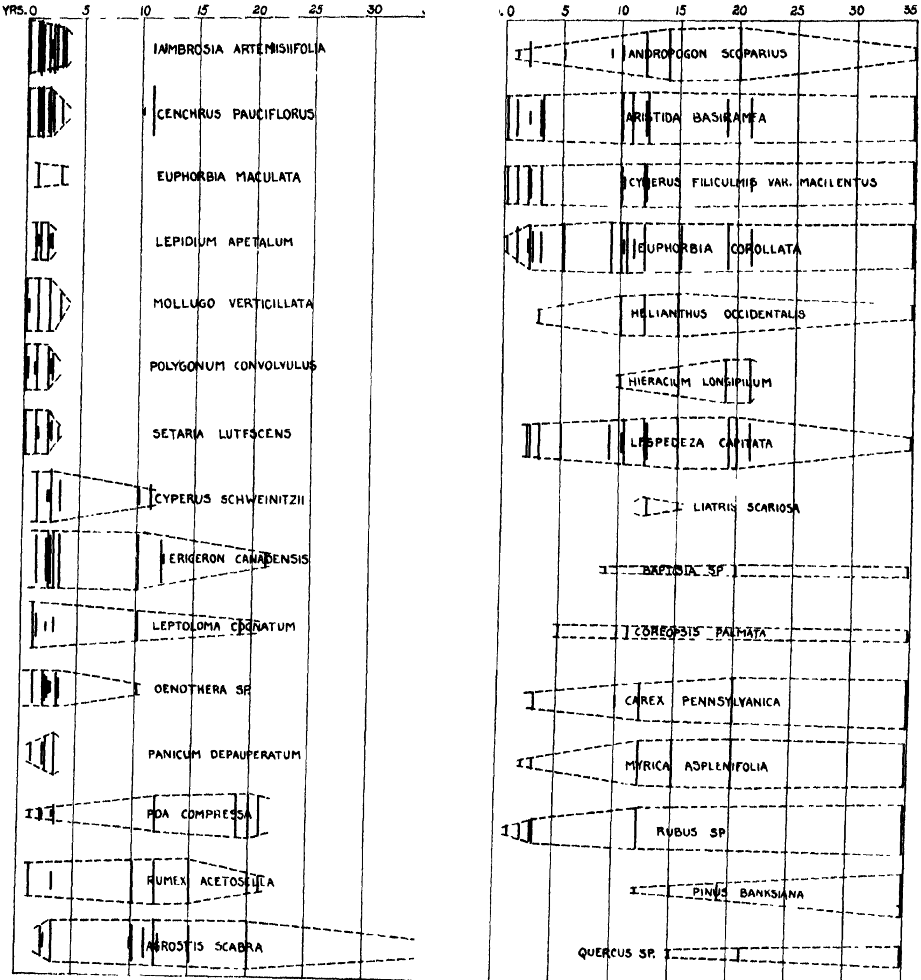


FIG. 1. Frequency of various species in abandoned fields.

scoparius. The prairie plants, however, do not attain any prominence in the early years; it is only at from nine to ten years after abandonment that they become important and they appear to reach a maximum in about fifteen years and thence show a slow decline until thirty-seven years, the age of the oldest field observed.

During the second year after the field is abandoned there is little change

to be observed. Ragweed, sandbur, and Canada fleabane remain the most important species. The prairie plants, represented by *Euphorbia corollata* and the *Andropogons*, have increased somewhat and a fourth species, *Lespedeza capitata*, appears as a prominent invader. Prairie plants are but a minor part of the flora in the fields at this stage; the weeds are still very prominent. *Hedeoma pulegioides*, *Agrostis scabra*, and *Physalis virginiana* appear, *Poa compressa* increases, and *Myrica asplenifolia*, which is later of great importance, gains a foothold. In one field, in T18N R3E S2NW, abandoned one year in 1936, sandbur was very abundant. In 1937 it had disappeared entirely but in 1938 it had again become prominent. This is rather exceptional, for sandbur is one of the critical species in the succession. In most of the fields observed this species disappeared after two years and none was present in fields abandoned for three years or more except where the fields had been disturbed. In the older fields sandbur appears as a result of heavy grazing, as it did in a ten-year field, or as a result of some other disturbance such as driving a car or wagon across the field. Sandbur then appears in the ruts. An attempt was made to see if the seeds of this plant remained viable in the soil and then germinated after disturbance by taking some of the soil of a field which had been abandoned for twenty-two years and placing it in shallow trays in the greenhouse. Several months afterwards, *Mollugo verticillata*, *Rumex Acetosella*, *Poa compressa* from the rhizomes, and *Antennaria* sp. had appeared but sandbur had not. It would be interesting to know how long the seeds of this species can remain viable while buried in the soil. The rapidity with which it becomes established in freshly cultivated fields on the sandy soils in this county is remarkable. The lesser ragweed, *Ambrosia artemisiifolia*, presents a situation comparable to the sandbur. It is abundant during the first three years following abandonment, then practically disappears, persisting in the fields only as a result of grazing or some other disturbance. Since this is a valuable game bird food plant, it is important that some fields under cultivation, or abandoned for not more than three years, be available as a food reserve on game preserves in this area.

Three years after abandonment the amount of ragweed decreases slightly and Canada fleabane becomes more dominant. *Lespedeza capitata* becomes slightly more common. *Oenothera biennis* has also risen in frequency. *Aristida basiramea*, *Asclepias tuberosa*, *Helianthus occidentalis*, and *Carex pensylvanica* are the important new invaders. As already mentioned, *Cenchrus pauciflorus* has disappeared in most fields except in disturbed spots.

In the one field observed five years after abandonment *Lespedeza capitata* and *Euphorbia corollata* had increased greatly. Four other prairie species appeared in the field: *Coreopsis palmata*, *Asclepias tuberosa*, *Litho-*

spermum gmelini, and *Andropogon scoparius*. These were not abundant. The observer unfortunately made no note of the weed flora in the field.

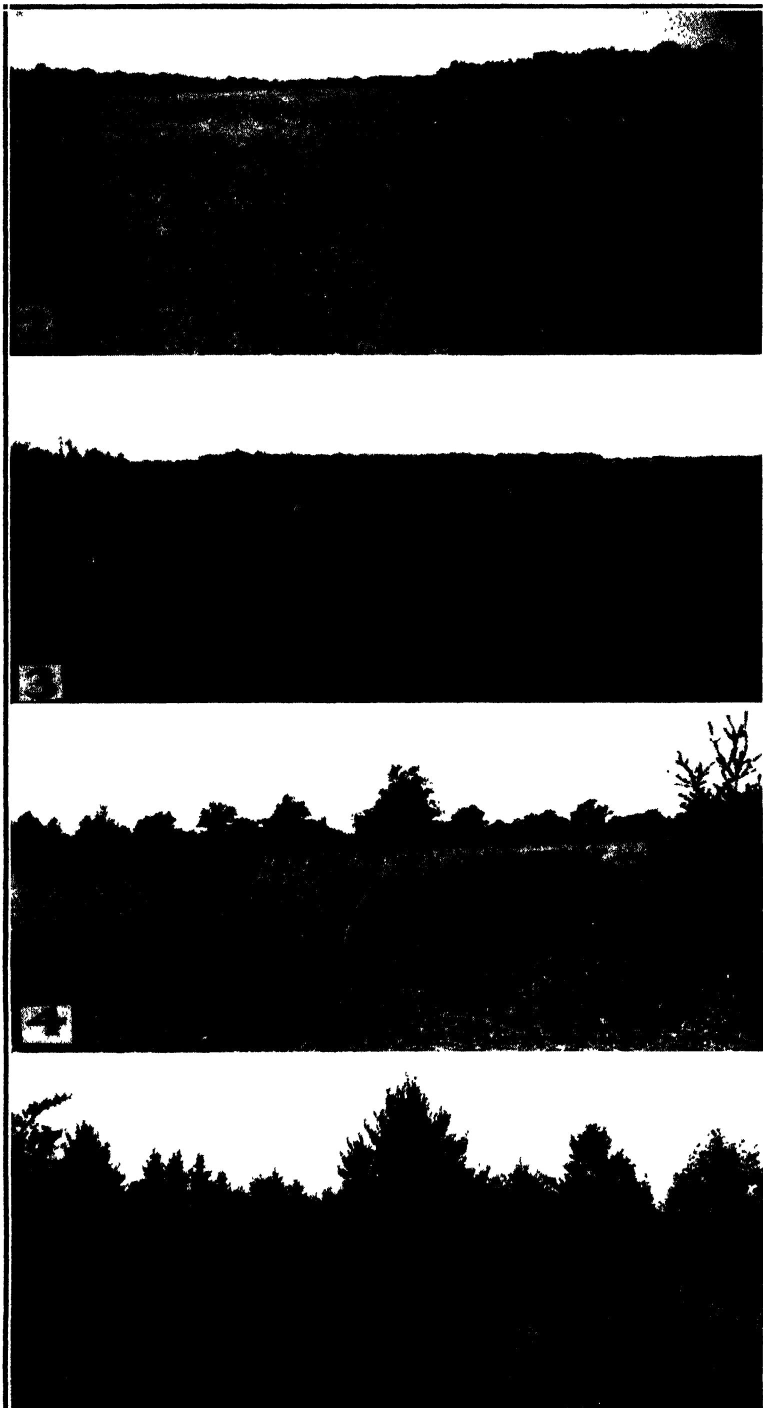
In fields which have been abandoned for nine or ten years the change in successions has slowed up somewhat. They are quite similar to four- or five-year abandoned fields, although the prairie species have increased in general in numbers of plants and of species. *Hieracium longipilum*, *Baptisia leucophaea*, and *Desmodium illinoense* have appeared. *Euphorbia corollata* and *Lespedeza capitata* have become important, but there is still much *Aristida basiramea* and *Erigeron canadensis*.

The single observed field of eleven years age of abandonment had been so heavily grazed that the succession upon it could hardly be termed typical. The hooves of cattle had so cut up the soil that great quantities of sandbur were present and the plants remaining in the field were mostly species unpalatable to cattle.

Twelve-year fields show an increase in the plants of the prairie species, especially of *Andropogon scoparius*, *Lespedeza capitata*, and *Euphorbia corollata*. *Erigeron canadensis* and *Aristida basiramea* begin to drop in importance. *Pinus banksiana* appears in fields of this age and increases from this time on. The patches of *Rubus* sp. and *Myrica asplenifolia* are becoming conspicuous. By the time the fields have been abandoned for fifteen years the prairie species have reached their maximum both in number of individuals and in number of species present in the fields. There is a fairly solid turf of *Andropogon scoparius*. *Lespedeza capitata* and *Euphorbia corollata* are very common. *Hieracium longipilum*, *Liatris scariosa*, *Helianthus occidentalis*, and *Lupinus perennis* var. *occidentalis* are present. Up to this time in the succession the distribution of each species has been fairly even throughout the field but now the various species begin to appear in patches rather than evenly distributed. This tendency becomes more accentuated in the older fields. Probably this tendency is caused in part by the severe competition in the field and the micro-conditions within the field limit the distribution of each species. The dominance of the prairie species persists in the fields from fifteen to twenty-two years abandoned but in the older fields, although the same species are present, the patches of distribution of the major species become more pronounced and the shrubby and woody plants, *Myrica asplenifolia*, *Rubus* sp., *Rhus glabra*, and *Pinus banksiana* become more prominent. *Carex pensylvanica* becomes more common.

Explanation of figures 2–5

FIG. 2. A field abandoned one year, T2ON R5E S6. Ragweed is the most conspicuous plant. FIG. 3. A field abandoned three years, T18N R3E S2. *Agrostis scabra* showing as white patches in the foreground, *Lespedeza capitata* in the background. FIG. 4. A field abandoned fifteen years, T19N R2E S17. Note abundance of *Andropogon scoparius*, scattered *Pinus banksiana*. Dark area is *Myrica asplenifolia*. FIG. 5. A field abandoned thirty-five years, T19N R3E S27. Photo shows scattered *Andropogon scoparius*; vigorous invasion by *Pinus banksiana* and a single *Populus grandidentata* at right.


3
4

By the time the field has been abandoned for thirty-seven years the forest has encroached considerably on the prairie flora. Jack pine, *Pinus banksiana*, is the dominating member of the flora and *Populus grandidentata* is also present. Shrubby plants including *Myrica asplenifolia*, *Corylus americana*, young *Quercus ellipsoidalis*, and *Rubus* sp. occupy considerable territory. *Carex pensylvanica* is common in the slight depressions in the field, forming an almost continuous turf. The prairie species have dwindled in importance and are present only in a few scattered clumps of *Euphorbia corollata*, *Andropogon scoparius*, *Koeleria cristata*, and *Lespedeza capitata*. *Baptisia leucophaea* and *Coreopsis palmata* are present as a few plants. *Liatris scariosa* was growing near the field in the open scrub oak woods but not in the field itself.

Later succession can be but conjectured, since the oldest field upon which observations were made had been abandoned thirty-seven years. In this field and on several of the other abandoned fields, young oaks were growing. In an abandoned field in Monroe County, just west of Mather, there is a thick growth of jack pine but a few young oaks are present among them. Since the oaks are more tolerant of shading than the pine, they would survive until some accident to the pines would open up a space for growth of the oaks, when they would begin growing rapidly and shade out the younger pines which might start. In this way an interspersion of oaks and jack pine would result. Through the northern part of Juneau County the land which was cut over and then kept as stump pasture has reverted to oak and pine woods. The early surveys made in 1851 record mixed forests of oaks and pines. While some of the finest stands of white pine in the country were present in Juneau County, they were on the moister soils, and the forest at the time of settlement was a mixed one. Over most of the area on which the white pine formerly grew cultivation and fires which followed the lumbering have destroyed most of the organic matter in the soil. To restore the soil to a condition suitable for a flourishing stand of white pine over much of the area would require centuries. Accordingly it would appear that the climax of succession on the dry sandy soils in Juneau County would be a mixed forest of oak and jack pine. *Quercus ellipsoidalis*, *Q. velutina*, and *Q. macrocarpa* are the principal oaks involved in the succession.

The causes of the succession are not at all understood, nor why the changes in the flora during the first years after the field is abandoned are rapid while later changes are more gradual. In Iowa Shimek[3] found that the prairie plants had become established in a field ten years after it was abandoned but that thirty years were required for complete establishment. Here in Juneau County the succession of prairie plants is a little slower,

[3] **Shimek, B.** Papers on the prairie. Univ. Iowa Studies in Nat. Hist. 5: 1–36. 1925.

requiring fifteen years, and is never complete, since the forest closes in by the time a field has been abandoned for thirty-five years. The perennials of the prairie flora type may replace the annuals of the weed type in the early years because they are better able to start growth in the spring and because they have more efficient root systems. But the disappearance of such species as the lesser ragweed may be dependent upon the rapid oxidation of organic matter such as manure in the dry sandy soils. Obviously the nutrient requirements of the plants and their water and light relations ought to be investigated. Some inquiry should be made into the soil conditions as affecting the growth of the plants; for changes within the soil may be responsible at least in part for the floral succession. One such type of experimentation would be to test the growth of the various important plants in the succession on soil samples taken from fields of varying ages of abandonment in order to determine whether there is an effect of the soil on germination, on growth of the seedling or on growth of the mature plant. Both topsoil and subsoil would have to be tested.

SUMMARY

The plant succession on abandoned fields in Juneau County, Wisconsin, is from a weed flora the first few years, with rapid changes in the succession, to prairie plants which appear in numbers at from nine to ten years after the fields are abandoned, and reach a maximum at about fifteen years after the fields have been abandoned. Finally the prairie plants decline as the forest represented by jack pine and oak becomes the climax.

SUPERIOR STATE TEACHERS COLLEGE
SUPERIOR, WISCONSIN

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 42–49 JANUARY, 1943

THE TAXONOMY OF THE MONOGENERIC TRIBE ELVASIEAE (OCHNACEAE)

JOHN D. DWYER

In 1811 De Candolle described the genus *Elvasia*[1] with a single species, *E. calophyllea,* and placed it in the Ochnaceae. Planchon in describing in 1848 the genus *Hostmannia* related it to *Elvasia.* In a later work Engler made *Hostmannia* a subsection of *Elvasia,* combining it with Planchon's subsection *Euelvasia.* Van Tieghem, the first worker to introduce radical changes into the genus, divided *Elvasia* into 4 genera, grouping the quartet under the tribe Elvasieae (Elvasiées) and Hostmannieae (Hostmanniées) of the subfamily Elvasiodeae. Gilg in the most recent treatment of the genus (1825) elected to retain Engler's 2 subsections.

This study of the genus *Elvasia* is a sequel to the author's work on the American species of the Luxemburgieae.[2] Although fourteen collections of *Elvasia* form the basis of this study of seven species, apparently no more than nineteen collections of this genus are deposited in herbaria or are cited in the literature. Six of my specific descriptions are based on type material.

Elvasia is limited to British Guiana, Surinam, Venezuela, and Brazil. Several collections made in the western part of the State of Amazonas, Brazil, indicate that this may be the center of distribution of the genus. *Elvasia* includes moderately sized trees and shrubs; members of the genus are not reported as being of economic importance. According to Pittier, in his discussion following the original description of *E. caronensis,* this species is known among the natives as *Manteco de Agua.* The brief history of *Elvasia* suggests that its position in the Ochnaceae is a sound one. The general structure of the pistils points especially to its relationship with the large ochnaceous genus *Ouratea.* This is evidenced by its usually lobed and short-stipitate ovary with axillary placentation. Each cell of the ovary bears an ovule which in fruit develops into an exalbuminous seed. On the other hand its affinity with the tribe Luxemburgieae is manifested in the constantly slender, crowded, and immersed secondary veins of the leaf-blades, a character found in *Blastemanthus* and *Wallacea* of the Luxemburgieae. The scarious sepals and the oblong, basifixed, and early deciduous anthers borne on slender persistent filaments resemble those of several genera of this tribe. Perhaps the most important character linking the Elvasieae

[1] Named by De Candolle in honor of Francois Manuel D'Elvas, who was, in the words of the author (Ann. Mus. Paris **17:** 408. 1811) "jésuite portugais qui le premier a écrit sur l'histoire naturelle du Brésil."

[2] This study is at present in manuscript form.

and the Luxemburgieae is the distinct radial stigmas of the section *Euelvasia*, which are strikingly reminiscent of the sessile radiating stigmas of the *Cespedezia, Godoya*, and *Rhytidanthera* complex of the Luxemburgieae. The tribe Elvasiae stands apart from both the Ourateae and the Luxemburgieae because of the unique structure of its fruit. In this the homologues of the lobes of the ovary dilate laterally from a median disc as ray-like structures; a solitary basifixed seed develops in the hollow of the disc left by the abortion of the walls of the carpels.[3] The inconstant number of carpels found in several species of *Elvasia* is not found in the genera of the Luxemburgieae and Ourateae.

While intragenerically the author maintains the two subdivisions *Euelvasia* and *Hostmannia*, which are based on differences in the number of carpels, further study indicates that a break in *Euelvasia* is necessary on the basis of stigmatic differentiation coupled with variations in the number of stamens. A third division, *Euessequibensa*, is proposed in this paper. General studies on the family Ochnaceae make it clear that carpellary variations in the species of the American genera are rare. In my opinion the variation in stigmatic structure in *Elvasia* is an exception to this stability, and is of equal importance as the equally exceptional variation in the number of carpels within the same genus. It is an interesting fact that fruiting material has been described only from the section *Euelvasia*. Whether the asteroid type of fruit, which characterizes the two species of this section of the genus, is found in the 5 species of the two other sections only additional collections of fruiting materials will disclose. One may anticipate a non-asteroid type of fruit for the section *Hostmannia* in which the carpels are reduced in number to two.

KEY TO THE SECTIONS

Ovary 4–5 celled; filaments of stamens (at late anthesis) not exceeding the anthers in length.

Stamens 7–10; stigmas 4–5, fimbriate, radial (0.1–0.25 mm. long) 1. *Euelvasia*.

Stamens 10–20 (rarely up to 25); stigmas undifferentiated 2. *Euessequibensa*.

Ovary 2-celled; filaments of stamens (at late anthesis) exceeding the anthers in length 3. *Hostmannia*.

KEY TO THE SPECIES

1. *Euelvasia*

Leaf-blades dull-brown above.

Sepals 3, 2.3–3 mm. long; petals 3–3.3 mm. long; stamens 7–8, the filaments 1.3–2.2 mm. long; disc of fruit not obvious, the rays distinctly marcescent rugose, 2–3 mm. wide at base 1. *E. calophyllea*.

Sepals 4, 3.8–5 mm. long; petals 4–4.8 mm. long; stamens 10, the fila-

[3] Van Tieghem (Ann. Sci. Nat. VIII 16: 408. 1902) gives an excellent description of the development of the fruit.

ments 0.4–0.8 mm. long; disc of fruit obvious, the rays almost smooth, 4–5 mm. wide at base 2. *E. quinqueloba.*
Leaf-blades cinero-canescent above 3. *E. canescens.*

2. *Euessequibensa*

Leaf-blades 6–8 cm. long; branches of inflorescence subhorizontal, obviously unequal 4. *E. brevipedicellata.*
Leaf-blades 9–20 cm. long; branches of inflorescence arcuate-ascending, subequal in length 5. *E. essequibensis.*

3. *Hostmannia*

Sepals subrotund or ovoid-rotund, 2.8–3.8 mm. long; petals 4.6–5.6 mm. long 6. *E. carunensis.*
Sepals elliptic to obovate-oblong, 5.5–6.5 mm. long; petals 6–9 mm. long. 7. *E. elvasoides.*

The materials cited in this paper have been secured from various American institutions which are designated by the following symbols:

F—Field Museum, Chicago, Ill.
G—Gray Herbarium, Cambridge, Mass.
NY—New York Botanical Garden, New York City, N. Y.
US—United States National Herbarium, Washington, D. C.

The author wishes to express his appreciation to the directors of the institutions listed above for their kindness in loaning him specimens. Special thanks are due to Dr. A. C. Smith of the Arnold Arboretum for his criticism of the manuscript.

ELVASIA DC. Ann. Mus. Paris **17**: 422. 1811.

Hostmannia Planch. in Hook Ic. Pl. **8**: pl. 709. 1848. *Vaselia* van Tieghem, Ann. Sci. Nat. VIII **16**: 409. 1902. *Trichovaselia* van Tieghem, Ann. Sci. Nat. VIII **16**: 411. 1902.

Trees or shrubs; leaf-blades subsessile or short-petiolate, coriaceous, acuminate, rarely retuse at apex, obtuse to cuneate at base, the costa slender and ridge-like, prominent, strigose, and hemispherical in cross-section below, becoming evanescent and plane toward apex, the secondary veins immersed, slender, crowded, leaving costa sub-horizontally, the margin entire, subcallose, often with minute, appressed, glandular teeth; stipules persistent or deciduous, deltoid to acute, axillary; buds subrotund to ovoid; inflorescence paniculate, terminal, the flowers solitary or in fascicles on slender, very short-articulate pedicels disposed on a smooth angular rachis terminating the twigs or rarely disposed on axillary branches, the bracts persistent or deciduous, carnose, oblong, very obtuse, the margin entire; sepals 3–5, quincuncial, carnose, reflexed or patent, soon deciduous at anthesis; petals 3–5, imbricate, carnose, reflexed or patent, deciduous at anthesis, yellow, the veins evanescent and flabellate toward margin, the latter entire; stamens 7–25, arranged in a circle about pistil, yellow, the anthers deciduous, 2-celled, dehiscing by 2 subterminal sub-auriculate pores usually slit-like at base, basifixed, the filaments free, slender, clavate at apex, persistent (even in young fruit); pistil solitary, the ovary short-stipitate, smooth or lobed, the carpels 2–5, fused, forming 2–5 cells, the ovules solitary per cell, oblong,

subplane, attached medianally or basally, the placentation axillary, the style persistent (up to immature fruit), subulate, the stigmas indeterminate or obviously 2 or disposed as 5 terminal radiate fimbriate projections of the style; fruit (known from two species) star-shaped, lignose, a single dorso-ventrally subplane exalbuminous seed developing in a single locule, the remaining ovules and carpellary walls aborting.

TYPE SPECIES: *Elvasia calophyllea* DC.

1. ELVASIA CALOPHYLLEA DC. Ann. Mus. Paris **17**: 422. 1811. *Elvasia sprucei* van Tieghem, Ann. Sci. Nat. VIII **16**: 409. 1902. *Elvasia schomburgki* van Tieghem, Ann. Sci. Nat. VIII **16**: 409. 1902.

Small trees; leaf-blades usually deflexed, often revolute, oblong-lanceolate, 4–6.5 cm. long, 2.5–4 cm. wide, tapering into an acuminate point or flat-obtuse at apex, obtuse-cuneate at base; stipules apparently persistent; inflorescence terminal, the rachis exceeding the uppermost leaves, up to 15 cm. long, the branches sub-horizontal, becoming shorter toward apex, the flowers dense, solitary or fasciculate on slender pedicels 3–8 mm. long, the bracts slender-subulate, 1–3 mm. long, deciduous; sepals 3–4, concave, obovate-rotund or obovate-oblong, 2.3–3 mm. long, 1.2–2.6 mm. wide, the veins subparallel, irregular-ascending, well-spaced and forming toward margin a loose flabellate reticulum; petals 4, subequal, oblong-rectangular or suboblong, 3–3.3 mm. long, 1.3–1.6 mm wide, round-obtuse toward apex, tapering slightly toward base, the veins evanescent; stamens 7–8, the anthers plump, ovate-oblong to narrow-ovoid, 1–1.3 mm. long, about 0.5 mm. wide at base, the filaments 1.3-2.2 mm. long; pistil stipitate (for about 0.2 mm.), 4–5-lobed and -celled, rhomboid in outline, about 1 mm. wide, the style 1.3–2.8 mm. long, somewhat swollen at base, bearing 5 radial and fimbriate stigmas at apex, each stigma about 0.2 mm. long; fruit dull gray-black, 4–5-rayed, up to 2 cm. in diameter, the rays distinctly rugose and contorted, unequal, the disc scarcely evident, the seeds orbicular, about 2.5 mm. wide, depressed above.

Type Locality: Brazil.

Illustration: DC. Ann. Mus. Paris 17: *pl. 31.* 1811.

Distribution: Known from British Guiana and the State of Amazonas, Brazil. BRITISH GUIANA: *Schomburgk 910* (F, photo and frag., G, type collection of *E. Schomburgki*), *Schomburgk 911* (?) (F). BRAZIL: Without definite locality or collector, labelled De Candolle (F, photo and frag. of type of *E. calophyllea*); AMAZONAS: Barra, Rio Negro, *Spruce 1792* (F, photo, G, photo, NY, type collection of *E. Sprucei*); Santa Izabel, *Ducke 56* (F, NY).

A thorough search of the literature, including the monograph in which the original description is found, failed to reveal the collector of the type material or the exact locality in which the type was collected. *E. calophyllea*, the type species is the most collected member of the genus. The reduction in the number of stamens (7–8) is its most outstanding specific floral character.

2. ELVASIA QUINQUELOBA Spruce ex Engler in Mart. Fl. Bras. **12** (2): 353. 1876. *Vaselia quinqueloba* van Tieghem, Ann. Sci. Nat. VIII **16**: 409. 1902.

Trees (?); leaf-blades often revolute, oblong, 10–15 cm. long, 3–5 cm. wide, acute at apex, cuneate at base; stipules persistent or deciduous, 2–3

mm. long; buds obovate-oblong, about 4 mm. long; panicle exceeding uppermost leaves, pyramidal, the branches subhorizontal, the pedicels about 3 mm. long, the lowermost bracts often persistent, narrow-subulate, 2.5–3 mm. long, very acute; sepals 4, concave, oblong, ovate-oblong or rectangular, 3.5–5 mm. long, 1.5–3 mm. wide, obtuse at apex and base, the veins few, well-spaced, parallel-ascending, flabellate toward margin; petals 5, obovate-oblong, 4–5 mm. long, 2–2.5 mm. wide, obtuse at apex, cuneate at base; stamens 10, the anthers linear-rectangular, about 3.5 mm. long, about 0.8 mm. wide, the filaments 0.4–0.8 mm. long; ovary smooth or distinctly lobed, 3–5-celled, rhomboid or subrotund in outline, about 0.9 mm. long, often wider than long, the style slender-subulate or thick-subulate (up to 0.5 mm. wide at base), 3–3.5 mm. long, the stigmas 5, fimbriate, radial, each stigma about 0.15 mm. long; fruit 4–5-lobed, 1–1.5 cm. in diameter, the rays red-brown, subsmooth, 3–5 mm. wide at base, the partitions persistent above, slender prominent, the seed about 6 mm. wide.

Type Locality: Rio Guainia and Rio Negro, above mouth of Rio Casiquiare, Amazonas, Brazil.

Illustration: Engler in Mart. Fl. Bras. **12** (2): *pl. 71. f. 1.* 1876.

Distribution: Known only from the type locality. BRAZIL—AMAZONAS: Rio Guainia and Rio Negro, above mouth of Rio Casiquiare, *Spruce 3513* (*3398*) (F, G, photo and type collection).

This species is obviously related to *E. calophyllea;* it is distinguished from the latter by being stouter in all its parts and by its distinctly oblong leaves.

3. ELVASIA CANESCENS (van Tieghem) Gilg in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **21**: 77. 1925. *Trichovalesia canescens* van Tieghem, Jour. de Bot. **16**: 205. 1902.

Small trees, 4–5 m. high; leaf-blades ashen-brown or waxy-farinose above, canescent, brown beneath, obovate-oblong, about 5 cm. long, 2 cm. wide, flat-obtuse to deltoid (often retuse and truncate) at apex, subcuneate at base, the margin with minute purple hairs about 1 mm. apart, curved downward; stipules persistent, subdeltoid, about 1 mm. long, about 1 mm. wide at base, acuminate; panicle terminal, pyramidal, about 8 cm. long, the branches slender, subhorizontal, densely flowered, the flowers solitary, the pedicels about 5 mm. long, the bracts concave, narrow-deltoid or subulate, about 3 mm. long; sepals 3–4, unequal, reflexed at anthesis, obovate-oblong or oblong, 2.3–4.3 mm. long, 1.2–2.7 mm. wide, obtuse to flat-obtuse at apex, obtuse at base, the veins 3–6, conspicuous or evanescent, branching flabellately above middle; petals 3–5, unequal, obovate-oblong or oblong, 2.6–5 mm. long, 1.3–2.5 mm. wide, round-obtuse or deltoid at apex, obtuse-cuneate at base, stamens 7–12, the anthers plump, linear-ovoid to elliptic, 1.35–1.5 mm. long, 0.5–0.8 mm. wide, the filaments 0.7–1.6 mm. long; pistil stipitate, the stipe 0.1–1 mm. long, the ovary 4–6-lobed, the lobes drooping, compressed-rhomboid in shape, 0.5–1 mm. long, 0.8–1.1 mm. wide, the style thickly subulate, 1.4–4.5 mm. long, the stigmas 4–6, terminal, radial, and fimbriate; fruit not seen.

Type Locality: San Fernando, Atabapo, Amazonas, Venezuela.

Distribution: Known from the type locality and from the state of Amazonas, Brazil. VENEZUELA—AMAZONAS: San Fernando, Atabapo, *Gaillard*

168 (F, photo and frag. of TYPE). BRAZIL—AMAZONAS: Rio Curicuriary and Rio Negro, *Ducke 356* (F).

Of the seven species of *Elvasia* listed in this paper, *E. canescens* is the most easily recognized, because of the distinctly canescent upper surface of the leaf-blade.

4. ELVASIA BREVIPEDICELLATA Ule, Notizbl. Bot. Gart. Berlin **6**: 339. 1915.

Trees 5–10 m. high; leaf-blades oblong, 6–8 cm. long, 2.5–3.5 cm. wide, acuminate at apex, wide-cuneate at base; panicle 3–5 cm. long, shorter than leaf-blades, the branches unequal, very short, the pedicels 3–4 mm. long; sepals 4 or more, about 6 mm. long, 4 mm. wide; petals subequal in length, spatulate-elliptic, about 6 mm. long, 4 mm. wide; stamens 20–25, the anthers exceeding the filaments in length, the latter about 1 mm. long, the anthers about 2.5 mm. long; ovary 5-celled, ovoid, about 1 mm. long, the style filiform, about 2 mm. long; fruit not seen.

Type Locality: Mt. Roraima, 1900 m. alt., British Guiana-Venezuela boundary.

Distribution: Known only from the type locality. BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Roraima, 1900 m. alt., *Ule 8664* (G, photo of type).

While the above description is based on a photograph of the type and on Ule's original description, there seems to be no doubt that this species is related to *E. essequibensis* Unfortunately Ule does not discuss its stigmatic structure, but the number of stamens surrounding 5 carpels is a strong indication of its relationship with *E. essequibensis*.

5. ELVASIA ESSEQUIBENSIS Engler in Mart. Fl. Bras. **12** (2): 354. 1876.

Hostmannia essequibensis van Tieghem, Ann. Sci. Nat. VIII **16**: 414. 1902.

Small trees or shrubs; leaf-blades dull gray-brown above, oblong, 9–20 cm. long, 3.5–8 cm. wide, conspicuously attenuate-apiculate at apex, the blade frequently splitting along the secondary veins, the margin subrevolute, entire, with minute black-glandular teeth, up to 0.5 mm. long; stipules persistent, elongate-deltoid, 3–5 mm. long, acute; buds rotund or oblong, about 3 mm. long at maturity; inflorescence terminal, patent-paniculate, the flowers in dense fascicles on the arcuate-ascending subequal branches, the latter equal to or exceeding the uppermost leaf-blades, the pedicels 2–4 mm. long, the bracts widely subulate, up to 3 mm. long, attenuate at apex; sepals 5, unequal, oblong, oblong-rectangular or obovate-oblong, 2.8–4.2 mm. long, 2–2.3 mm. wide, obtuse at apex, obtuse to subcuneate at base, the veins 6–8, conspicuous, well-spaced; petals 5, oblong-obovate, obovate-rotund or oblong, 4.7–5 mm. long, 2.3–4.3 mm. wide, obtuse (frequently retuse) at apex, subobtuse to cuneate at base, the median veins distinct, the lateral veins usually evanescent and flabellate; stamens 11–18, the anthers linear-rectangular, 2.2–3.2 mm. long, 0.5–0.8 mm. wide, the filaments 1–1.3 mm. long; ovary very short-stipitate, the stipe up to 1 mm. long, 4–5-celled, 0.7–1.3 mm. long, the style 2–4.5 mm. long, often contorted or transverse-rugose, constricted and markedly truncate at apex, the stigmas a plane surface; fruit not seen.

Type Locality: Essequibo River, British Guiana.

Illustration: Engler in Mart. Fl. Bras. **12** (2): *pl. 71, f. 2.* 1876.

Distribution: British Guiana. BRITISH GUIANA: Mazaruni & Cuyuni Rivers, *Graham 153* (NY); Essequibo River, *Jenman 1325* (NY).

This species is readily recognized by its constantly large and markedly oblong leaf-blades and arcuate-ascending branches of the inflorescence.

6. ELVASIA CARUNENSIS Pittier, Bol. Soc. Venez. Cien. Nat. **6** (41): 75. 1939.

Trees up to 15 m. high, the branches above middle of trunk; leaf-blades narrow-lanceolate, 7–15 cm. long, 2.5–4.6 cm. wide, acute and narrowly acuminate at apex, cuneate at base; stipules deciduous, striate, deltoid, up to 5 mm. long, the free lobes deltoid and long-acuminate; buds rotund, about 2.5 mm. wide; inflorescence terminal, not exceeding uppermost leaves in length, pyramidal, the flowers fasciculate on the horizontal whorled branches, the pedicels long, the bracts subconcave, widely subulate-deltoid, up to 3 mm. long; sepals 3–4 smooth, unequal, subrotund or ovoid-rotund, 2.8–3.8 mm. long, 2.6–3 mm. wide, obtuse at apex and base, the veins parallel-ascending, well-spaced, branching loosely above middle; petals 3–4, reflexed at anthesis, obovate or obovate-oblong, 4.7–5.6 mm. long, 2.2–3.3 mm. wide, obtuse at apex and base, the veins flabellate and immersed; stamens 15–21, the anthers plump, ovate-oblong, 2–2.3 mm. long, about 1 mm. wide, the filaments 1.2–2.5 mm. long; ovary smooth, rotund or rhomboid, 1.2–2.4 mm. long, 1.2–1.5 mm. wide, 2-celled, 2-ovuled, the style thick-subulate or slender and contorted, 1.7–7.5 mm. long, the stigmas undifferentiated or the style grooved above the middle and bearing two lateral stigmatic surfaces at apex; fruit not seen.

Type Locality: El Pescado, Bolivar, Venezuela.

Distribution: Known only from the type locality. VENEZUELA—BOLIVAR: El Pescado, 140 m. alt., *Llewelyn Williams 11525* (F, NY, type collection).

Pittier, in his discussion following the original description of *E. carunensis*, states that the number of stamens is constantly 17. My counts of the stamens in type material show them to vary from 15–21. This species shows its close relationship with *E. elvasoides* in its vegetative habit as well as in the number of the stamens, length of the filaments, number of the cells of the ovary, and its stigmatic differentiation. Notable differences are apparent: *E. carunensis* has smaller flowers, subrotund or ovoid-rotund sepals, and the usually rhomboid-shaped ovary.

7. ELVASIA ELVASIODES (Planch.) Gilg in Engler & Prantl. Nat. Pflanzenfam. III **6**: 145. 1893. *Hostmannia elvasiodes* Planch, in Hook Ic. Pl. **8**: pl. 709. 1848. *Elvasia Hostmannia* Planch. Lond. Jour. Bot. **5**: 648. 1846. *Hostmannia Sagoti* van Tieghem, Ann. Sci. Nat. VIII **16**: 414. 1902.

Trees; leaf-blades oblong to oblong lanceolate, 5–8 cm. long, 2-3.5 cm. wide, abruptly acuminate at apex, cuneate at base; stipules persistent, blackish, widely subulate, 3–4 mm. long, the margin erose; buds subrotund, about 4 mm. long at maturity; inflorescence terminal or on axillary branches, equal to or exceeding the uppermost leaf-blades in length, compressed pyramidal-paniculate, the branches subhorizontal or obviously ascending, the flowers dense, solitary or fasciculate, the pedicels slender, 4–9 mm. long, the bracts concave, oblong or rectangular, about 3 mm. long, the margin hyaline or somewhat irregular; sepals 4, reflexed at anthesis, thin-carnose, subequal in length and width, elliptic to obovate-oblong, 5.5–6.5 mm. long, 3–3.5 mm. wide, obtuse to subdeltoid at apex, obtuse to subcuneate at base, the veins about 6, well-spaced and parallel-ascending; petals 4, thin-carnose,

unequal, reflexed at anthesis, obovate-spatulate, obovate-oblong, or obovate, 6–9 mm. long, 3–4 mm. wide, obtuse at apex, wide-cuneate to obtuse at base, the veins few subflabellate from a somewhat swollen midvein; stamens 17–21, the anthers oblong, about 3 mm. long, 1 mm. wide, the filaments slender, 2–3.6 mm. long, exceeding anthers in length; ovary smooth, vaguely lobed, ovoid-rotund in outline, 1.1–1.6 mm. wide, the style subplane, subulate, thickened toward base, 2-grooved above middle, 5–6 mm. long, the stigmas 2 or simply indeterminate, the ovary 2-celled, the 2 ovules about 0.8 mm. long, attached sub-basally; fruit not seen.

Type Locality: Dutch Guiana.

Illustration: Planch. in Hook. Ic. Pl. **8**: *pl. 709.* 1845.

Distribution: French and Dutch Guianas. DUTCH GUIANA: *Hostmann 271* (F, type collection); Marowyne River, *Kappler 1725* (F). FRENCH GUIANA: Karouany, *Sagot 786* (F, photo and frag. of TYPE of *Hostmannia Sagoti*).

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 50–52 JANUARY, 1943

KAIETEUREA, A NEW GENUS OF THE OCHNACEAE

JOHN D. DWYER

Kaieteurea Dwyer, gen. nov. Arbores vel suffrutices; laminae simplices, subsessiles ad apicem ramulorum persistentes coriaceae, costa supra infraque prominente, venis secundariis evanescentibus prominulis vel submersis, margine integro; gemmae ovoideae; stipulae ovoideae caducae; inflorescentia terminalis floribus solitariis, alibus in ramis racemosis axillaribus et alibus in paniculatis rhachidibus virgas terminantibus dispositis, pedicellibus recurvatis gracilibus, bracteis persistentibus aut caducis parvis obtusis margine integro; sepala 2 (rare 3), opposita aut alterna in gemma concrescentia marginibus non-imbricatis carnosa persistentia (in etiam fructu); petala 3–4 mox decidua carnosa oblonga margine integro; stamina 10, antheris mox deciduis transverse-rugosis lineari-rectangularibus 2-poris terminalibus dehiscentibus, filamentis liberis subnullis; pistillum solitarium, ovario stipitato in annulum 5 carpellis dispositis 5-locularibus ovulo solitario in utroque loculo, stylo uno terminale subulato, stigmatibus nullis; fructus stipitatus solitaria drupa dispositus rotundatis sepalis involutus, semini solitario exalbuminoso.

Trees or shrubs; leaf-blades simple, subsessile, persistent at the apices of the branches, coriaceous, the midrib prominent above and below, the lateral veins evanescent or immersed, the margin entire; buds ovoid; stipules deciduous; inflorescence terminal, the flowers solitary, some arranged on racemose axillary branches, others on a paniculate rachis terminating the twiglets, the pedicels slender, recurved, the bracts persistent or deciduous, small, obtuse, the margin entire; sepals 2, (rarely 3), fused in bud, opposite, carnose, persistent (even in fruit); petals 3–4, soon deciduous, carnose, oblong, the margin entire; stamens 10, the anthers soon deciduous, transversely rugose, linear-rectangular, dehiscing by two terminal pores, the filaments free, scarcely measurable; pistil solitary, the ovary stipitate, 5-carpellate, the carpels arranged in a ring, 5-celled, a single ovule in each cell, the style solitary, terminal, subulate, the stigmas non-differentiated; fruit stipitate, solitary, drupaceous, rotund, enclosed by the persistent sepals, the seed solitary, exalbuminous.

Carpellary studies leave no doubt that *Kaieteurea* is related to the ochnaceous genus *Ouratea*, well-known to workers in the floras of the new and old worlds. The five fused and uniovulate (one ovule per locule) carpels arranged in a circle atop a conspicuous stipe and terminated above by a subulate style with undifferentiated stigmas are unmistakably similar in both genera. *Kaieteurea*, while similar to *Ouratea* in vegetative habits and structure, shows marked differences in its fruit and flowers. In fruit, the torus becomes lignose, scarcely expands, and bears a single drupe encased in the two erect persistent sepals. The absence of endosperm in the seed places *Kaieteurea* together with *Ouratea*, *Ochna*, *Brackenridgea* (Ourateae), and *Elvasia* (Elvasieae) in the primary subdivision of the Ochnaceae, Exalbuminosae. On the basis of fruit structure further study may prove that *Kaieteurea* is deserving of tribal rank. The floral differences are equally

striking. The new genus, unlike any other American genus of the Ochnaceae, frequently has one pair of opposite sepals; this is a marked deviation from the quincuncial arrangement of the sepals which typifies *Ouratea*, *Elvasia*, and the majority of the genera of the Luxemburgieae. The marked reduction in the number of sepals to 2 is a condition not met with in the above genera and tribe. Critical examination of the margins of the sepals of *Kaieteurea* shows that these are fused in the bud and at anthesis are torn apart. The persistence of the sepals as well as their erect habit in the fruit point to the relationship of the new genus to the Luxemburgieae, many of whose genera have the sepals persistent and erect in the fruit. Accompanying the marked reduction in the number of sepals is a frequent reduction in the number of petals to 3. *Ouratea*, with the exception of odd and obviously abnormal flowers, is distinctly pentamerous. The biporous, linear-rectangular, and transversely rugose anthers of *Kaieteurea*, which are borne on scarcely measurable filaments and disposed in a single circle at the base of the stipe, are the prototypes of those of *Ouratea* This relationship is further manifested in the constancy in the number of the stamens.

Kaieteurea derives its name from the Kaieteur Savanna, British Guiana, where the type-species was collected. Potaro Landing, Kaieteur Savanna, is the home of a considerable number of endemics.

Kaieteurea gillyana Dwyer, sp. nov. Arbores vel suffrutices; folia ad apicem ramulorum conferta; petiolo brevi, circular 3–8 mm. longo suffulta, lamina ascendente coriacea brunnea rigida glaberrima oblonga, 3–5 cm. longa, 1.2–2.5 lata, ad apicem et ad basim distincte cuneata, costa supra in culminem elevata, circ. 0.5 mm. lata, supra prominente infra longitudino-striata ad basim circ. 2 mm. lata apice evanescente, nervis secundariis subobscuris, alibus paucis distantibus arcuato-ascendentibus prominulis juxta costam margine subprominentibus, alibus multis crebris irregularibus a costa ad angulum 80° abeuntibus, margine integro; gemmae ovoideae, circ. 5 mm. longae, acutissimae; inflorescentia ad apicem virgarum multis ramis racemosis ab superiorum laminarum axillis singulatim orientibus et in modum paniculae caulem extrahentis disposita latidudine subaequalibus et vix longioribus superioribus rhachidibus ramisque lignosis angularibus striatis subtortisque, floribus crebris, pedicellis recurvatis, 0.5–1 cm. longis, gracili-marcescenti-striatis singulatim dispositis, bracteis persistentibus aut deciduis concavis oblongis, circ. 1.5 mm. longis; sepala 2 (rare 3), opposita persistentia (in etiam fructu) rubro-brunnea carnosa longitudine vix marcescenti-striata ovata vel ovato-rotunda, 5.5–6 mm. longa, 4.5 mm. lata, ad apicem late deltoidea ad basim obtusa; petala 3–4 subaequalia caduca carnosa rubro-brunnea (?) oblonga, circ. 7.5–8 mm. longa, 3–3.9 lata, ad apicem obtusa retusaque (sinu circ. 0.5 lata) ad basim obtusa; stamina 10, uniseriata, anthera transverse-rugosa rubra lineari-rectangularibus saepe in medio geniculatis, circ. 5.5 mm. longis, ad basim 1–1.5 mm. latis, 4-locularibus interioribus (eorum) vix brevioribus angustioribus ad apicem biporosis; pistillum solitarium stipitatum (stipite 0.5–1 mm. longo), ovario carnoso 5-loculare 5-ovulato aequale distincteque lobato, depresso-rotundo, circ. 1.5 mm. lato, circ. 0.6 mm. longo, ovulis loculos complentibus sublongis, circ. 0.5 mm. longis, basifixis, stylo-filiformi, circ. 4 mm. longo, stigmatibus nullis; fructus stipitatus (stipite recto nigro lignoso mar-

cescente clavato, circ. 2.5 mm. longo, apice 2.5 mm. lato) vix marcescens rotundatus sepalis involutis, semini solitario exalbuminoso.

Distribution: Known only from the type locality. BRITISH GUIANA: Potaro Landing, Kaieteur Savanna, *Jenman 863* (NY TYPE).

This species is named for Mr. Charles Gilly of the New York Botanical Garden who by his criticism assisted the author in his preliminary constructive work on the Ochnaceae.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 53–57 JANUARY, 1943

THE STATUS OF DISTICHLIS DENTATA

JOHN R. REEDER

While studying grasses collected in Eastern Oregon in the summer of 1941, the writer was impressed with the difficulty of separating *Distichlis dentata* Rydb. and *D. stricta* (Torr.) Rydb. None of the available keys was satisfactory and even the original description of *D. dentata* seemed vague. In view of this apparent confusion, a critical study was made of these two species and the conclusions reached are here presented.

For material kindly loaned for study, in addition to his own specimens and the collection at Oregon State College, the writer herewith expresses his appreciation to the United States National Herbarium, the Rocky Mountain Herbarium, and the University of Oregon. He is especially indebted to the New York Botanical Garden for the loan of types. Thanks are due also to Mrs. Agnes Chase for personal selection of specimens and for criticism of the manuscript and to Dr. Helen Gilkey for suggestions given throughout the progress of the study.

Rydberg (1909) described *Distichlis dentata* as differing from *D. stricta* and *D. spicata* "in the broader leaves, larger and broader spikelets, larger and broader floral glumes and palets in the pistillate plants, and in the distinct dentations on the keels of the latter." He cited collections from Washington, Oregon, Saskatchewan, and Nevada

Fassett (1925), commenting on Rydberg's description, states: "In all these characters *D. stricta* is extremely variable, and while the conspicuously dentate paleas appear at first to be distinctive, this character breaks down when it is seen that almost all of the plants have the lemmas[1] somewhat dentate, and there is a difference only of degree." He places *D. dentata* in synonymy with *D. stricta*.

Hitchcock did not recognize either *D. stricta* or *D. dentata* until some time after 1923. In his *Genera of Grasses* (1920) and in Abrams' *Illustrated Flora of the Pacific States*[2] (1923) both *D. stricta* and *D. dentata* are listed as synonyms of *D. spicata*. However, in his *Manual of Grasses* (1935), Hitchcock recognized both of these species. His maps show *D. stricta* occurring in every state west of the Mississippi except Arkansas and Louisiana; *D. dentata* is listed as occurring only in Washington, Oregon, Idaho, Colorado, Nevada, Arizona, Utah, and Northern California.

Detailed study of the types of *D. dentata* and *D. stricta*, as well as of specimens from 17 western states, convinces the writer that *D. dentata* is not

[1] This is obviously an error. The word "lemma" should be palea.
[2] Key to the Grasses by A. S. Hitchcock.

a good species. The problem is complicated by the fact that the genus *Distichlis* is dioecious. Comparison of specimens labeled *D. dentata* with those labeled *D. stricta* indicates that the former has been separated entirely on the basis of the characteristics of the pistillate plants. Table 1[3] is a comparison of these two species without regard to sex.

TABLE 1

	D. stricta	*D. dentata*
Leaf width in mm.	1.5–3.5	1.5–4.0
Florets per spikelet	5–18	5–13
Width of spikelet in mm.	3.0–5.5	4–6
Length of spikelet in mm.	8–27	10–20
Width of lemma in mm.	1.5–2.2	1.8–2.5
Length of lemma in mm.	4.0–7.5	4.5–7.0

It will be noted that all the characters compared above, with the exception of "florets per spikelet," were used by Rydberg to separate *D. dentata* from *D. stricta*. Examination of table 1, however, shows that there is so much overlapping that these characters are not diagnostic.

Hitchcock (1935), in his key, separated *D. dentata* from *D. stricta* on the basis of the dentate palea-keels plus relative length of lemma to palea.[4] In his description he stated that the panicles of *D. dentata* are usually "overtopped" by the leaves. The following table is a comparison of staminate and pistillate plants regardless of the name on the label.

TABLE 2

	Staminate	Pistillate
Keels broadly winged	–	+
Keel wings prominently serrulate	–	+
Panicles exceeding the leaves	+	–

Examination of the paleas of the pistillate plants labeled *D. dentata* revealed that none of them is strictly dentate, while all are serrulate or serrulate-lacerate. This is also true for the pistillate plants labeled *D. stricta*. In both of these "species" the width of the keel varies from extremely wide to rather narrow, but the wing is always evident. In the staminate plants the palea-wings are entire or very slightly serrulate,[5] and are always narrower

[3] The data presented here represent a compilation of measurements made on all the specimens studied.

[4] In the Manual, *D. dentata* is said to have paleas longer than the lemmas, in contrast to *D. spicata* and *D. stricta* in which the lemmas exceed the paleas. However, Mrs. Agnes Chase, in a letter to the writer's wife, says that this is an error and that the two statements should be reversed, i.e., *D. dentata* has paleas shorter than the lemmas.

[5] Under a magnification of 20 diameters or more, in addition to serrulations, fimbriations may also be seen on the wing-margins in both staminate and pistillate plants.

than in pistillate plants (fig. 1). It was further noted that the paleas are shorter than the lemmas in practically all spikelets of the pistillate plants of the genus; while in the staminate plants the paleas are usually as long as, or longer than, the lemmas. Also the panicles of staminate plants usually exceed the leaves, while in pistillate plants the leaves commonly "overtop" the panicles (fig. 2). It is readily seen that these characters, which have been used to separate species, are merely distinctions between the sexes.

A very significant fact disclosed by this study is that 100 per cent of all sheets labeled *D. dentata* contained pistillate plants; while only 30 per cent

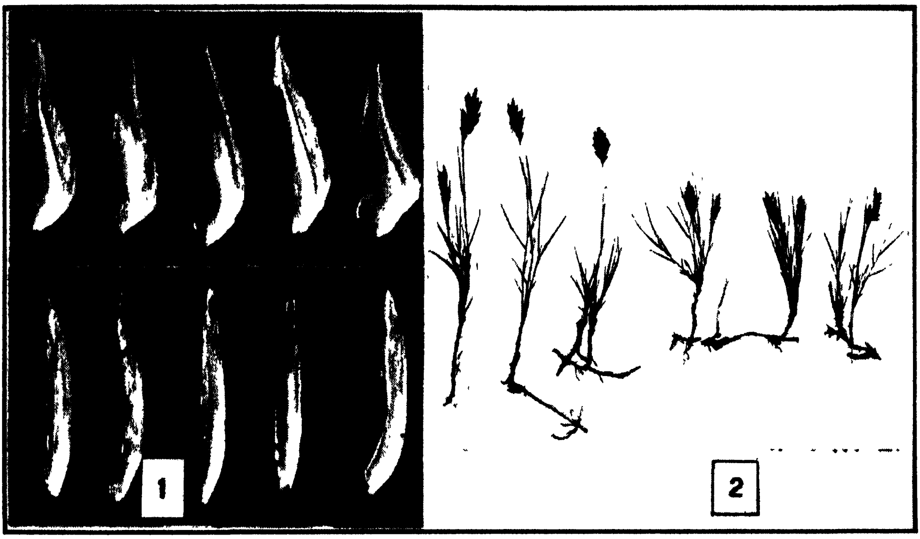


FIG. 1. Paleas of *Distichlis stricta* ×5. Pistillate above; note very wide keel wings and prominent serrulations. Staminate below; note narrow keel-wings and almost total absence of serrulations. FIG. 2. *Distichlis stricta*. Staminate plants on the left; note that the panicle is borne well above the leaves. Pistillate plants on the right; note that the leaves exceed the panicle.

of those labeled *D. stricta* contained pistillate plants. Indeed the type specimen of *D. dentata* is pistillate, while that of *D. stricta* is staminate.

Staminate plants were rare on sheets labeled *D. dentata;* when they were present they differed in no essential character from those on sheets labeled *D. stricta.* On the other hand, 70 per cent of the sheets labeled *D. stricta* contained staminate plants alone. Pistillate plants on the sheets labeled *D. stricta* often have all the characters described for *D. dentata*, although the width of the keel is variable as previously mentioned. However, when plants having the characters of *D. dentata* have been observed in the field by the writer, staminate plants have predominated. On numerous occasions it has required patient search before pistillate plants could be found. In view of these facts it seems obvious that *D. dentata* has been segregated from *D.*

stricta solely on the basis of the character of the pistillate plants. In almost any collection the pistillate plants could readily be referred to *D. dentata* and the staminate to *D. stricta*. This evidence indicates that *D. dentata* Rydb. should be reduced to synonymy under *D. stricta* (Torr.) Rydb.

SPECIMENS EXAMINED

Specimens from the following herbaria have been consulted in making this study: United States National Herbarium, Washington, D. C. (US); Oregon State College, Corvallis, Oregon (OS); University of Oregon, Eugene, Oregon (UO); Rocky Mountain Herbarium, Laramie, Wyoming (RM); and New York Botanical Garden, New York (NY).

CALIFORNIA: *Hitchcock 2586* (♂), US; *Silveus 2855* (♂), US. COLORADO: *Johnson 1031* (♀), as *D. dentata*, US; *Rollins 1957* (♂), US. IDAHO: *Chase 4767* (♂ & ♀), as *D. dentata*, US; *C. P. Smith 1772* (♂), US. KANSAS: *Thompson 25* (♂), US. MINNESOTA: *Hotchkiss & Jones 3997* (♂ & ♀), US. MISSOURI: *Bush 6460* (♀), US. MONTANA: *Williams & Griffiths 233* (♂), US. NEBRASKA: *Clements 2840* (♀), US; *Hapeman* in 1926 (♂), OS; *Rydberg 1814* (♂ & ♀), US; *Thomson 335* (♀), US. NEVADA: *Heller 10558* (♂ & ♀), as *D. dentata*, US; *Tidestrom 10147* (♂ & ♀), as *D. dentata*, US; *Train 2192* (♀), as *D. dentata*, US. NEW MEXICO: *Hardies* in 1936 (♀), US; *Dr. James*, sources of the Canadian (♂), (TYPE), NY. NORTH DAKOTA: *Hitchcock 5059* (♂), US; *Lunnell* in 1913 (♀), US. OKLAHOMA: *Clemens 11489* (♀), US; *Stevens 660* (♂), US. OREGON: *Anderson* in 1935 (♂), UO; *Cusick 1948* (♂ & ♀), UO; *Elder 143* (♂ & ♀), as *D. dentata*, US; *Fleischman* in 1934 (♀), OS; *Gilkey* in 1932 (♂ & ♀), OS; *Griffiths & Morris 501* (♂), US; *Henderson 8172* (♀), UO; *Ingram B673* (♂ & ♀), OS; *Ingram* in 1917 (♀), OS; *Johnson* in 1932 (♂), OS; *Kuehner* in 1927 (♂), OS; *Leiberg 463* (♀), UO; *712* (♂), US; *712* (♂ & ♀), UO; *2387* (♀), as *D. dentata*, US; *Parsell 269* (♂), OS. SOUTH DAKOTA: *Griffiths 355* (♀), US; *202* (♂), US; *Wallace 6* (♂), US. UTAH: *Garrett 5201* (♀), as *D. dentata*, US; *Harrison 293* (♂), US. WASHINGTON: *Elmer 508* (♀), as *D. dentata*, US; *Leckenby* in 1898 (♂), US; *Sandberg & Leiberg 251* (♂), US; *463* (♀), as *D. dentata*, US & RM (TYPE of *D. dentata* at NY); in 1893 (♀), as *D. dentata*, RM; *Sprague* in 1938 (♀), OS; *Vasey 4* (♂), US. WYOMING: *Merrill 12* (♂ & ♀), US; *Nelson 8175* (♂), US.

SUMMARY

Study of numerous collections of *Distichlis* from 17 western states shows that *D. dentata* is not distinct from *D. stricta*. These two "species" cannot be separated on the basis of staminate plants and only arbitrarily on the basis of pistillate plants. The basis for segregation of *D. dentata* has apparently been the characters of the pistillate plants, as no single collection of staminate plants has been referred to this species. *D. dentata* is reduced to a synonym of *D. stricta*.

DEPARTMENT OF BOTANY, OREGON STATE COLLEGE
CORVALLIS, OREGON

Literature Cited

Abrams, L. 1923. An Illustrated Flora of the Pacific States. Vol. 1. Stanford University Press. p. 194.

Fassett, N. C. 1925. Notes on Distichlis. Rhodora **27**: 67–72.

Hitchcock, A. S. 1920. The Genera of Grasses of the United States. U. S. Dept. Agric. Bull. 772. pp. 56–58.

——————. 1935. Manual of Grasses of the United States. U. S. Dept. Agric. Misc. Publ. 200. pp. 175–179.

Rydberg, P. A. 1909. *Distichlis dentata* sp. nov. Bull. Torrey Club **36**: 536.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 58–61 JANUARY, 1943

NEW NORTH AMERICAN UMBELLIFERAE—II

MILDRED E. MATHIAS AND LINCOLN CONSTANCE

Tauschia Johnstoniana Mathias & Constance, sp. nov. Herba acaulescens caespitosa, 10–15 cm. alta, scabrida vel scaberula; folia in ambitu oblonga vel ovata, petiolo excluso 2–6.5 cm. longa, 2–4 cm. lata, pinnata vel pro parte bipinnata, foliolis linearibus oppositis distinctis, 5–40 mm. longis, 1–1.5 mm. latis, integris mucronatis; petioli 3–5 cm. longi infra anguste scarioso-marginati; pedunculi 7–9 cm. longi, folia aequantes vel excedentes; involucri bracteae 1–2, lineares; involucellae bracteolae plures lineares, 1–5 mm. longae, circa flores aequantes, fructu breviores; radii fertiles 3–5, subaequales, 10–15 mm. longi scaberuli; pedicelli circa 1 mm. longi; flores lutei; styli tereti graciles recurvati; fructus ovalis circa 5 mm. longus, 2–3 mm. latus, commissurae apice alte excavata, costis filiformibus; vittae parvae in intervallis atque in commissura plures; seminis facies sulcata.

Acaulescent, caespitose, 10–15 cm. high, the foliage and inflorescence scabrous or scaberulous; leaves oblong to ovate in general outline, excluding the petiole 2–6.5 cm. long, 2–4 cm. broad, pinnate to partially bipinnate, the leaflets linear, opposite, distinct, 5–40 mm. long, 1–1.5 mm. broad, entire, mucronate; petioles 3–5 cm. long, narrowly scarious-margined below; peduncles 7–9 cm. long, equalling to exceeding the leaves; involucre of 1–2 linear bracts; involucel of several linear bractlets, 1–5 mm. long, about equalling the flowers but shorter than the fruit; fertile rays 3–5, subequal, 10–15 mm. long, scaberulous; pedicels about 1 mm. long; flowers yellow; styles terete, slender, recurved; fruit oval, about 5 mm. long, 2–3 mm. broad, with a V-shaped depression at the commissure, the ribs filiform; oil tubes small, several in the intervals and on the commissure; seed face sulcate.

TYPE: *Stanford, Retherford & Northcraft 682*, on mountain top 7 kilometers southwest of Miquihauana, Tamaulipas, Mexico, alt. 3430 m., August 5, 1941 (UC, TYPE; GH, isotype). Although it fully agrees with the chief generic characters, this very striking species does not seem to possess any close relatives. In our key it appears variously next to *T. Ehrenbergii* (Wolff) Mathias, *T. Stricklandi* (Coult. & Rose) Mathias & Constance and *T. texana* Gray, but these juxtapositions may be due fully as much to chance as to consanguinity. The species is named in honor of Dr. Ivan M. Johnston, of Harvard University, who is the author of some excellent critical studies of American Umbelliferae, and who correctly placed the present entity in the proper genus.

Lomatium idahoense Mathias & Constance, sp. nov. Plantae aculescentes vel brevi-caulescentes, 2–4 dm. altae, e radice prima gracile; caules graciles glabri; folia pauca glabra in ambitu obovata, petiolo excluso 4–12 cm. longa, ternato-pinnata vel pro parte biternata, divisionibus ultimis anguste linearibus vel oblongis acutis obtusisve, 1–10 cm. longis, 1–4 mm. latis; petiolus glaber, 1.5–12 cm. longus, parte inferiora (0.3–0.6 cm.) anguste vaginante; involucella nulla; radii 3–7 adscendentes, 2–8 cm. longi, inaequales graciles; pedicelli filiformes, 5–15 mm. longi; umbellularum flores 7–20 lutei; fructus glaber anguste oblongus ad apicem acutus, 10–12 mm. longus, 3–4 mm.

latus, alis quam corpore multo angustioribus; vittae in intervallis solitariae, in commissura 2.

Plants caulescent or short-caulescent, 2–4 dm. high, from a long, slender taproot, the stems slender, few-leaved, glabrous; leaves obovate in general outline, excluding the petiole 4–12 cm. long, ternate-pinnate or partially biternate, the ultimate divisions narrowly linear to oblong, acute or obtuse, 1–10 cm. long, 1–4 mm. broad, glabrous; petiole 1.5–12 cm. long, narrowly sheathing in the lower one- or two-thirds, glabrous; involucel wanting; rays 3–7, ascending, 2–8 cm. long, unequal, slender; pedicels filiform, 5–15 mm. long, the umbellets 7–20-flowered; flowers yellow; fruit narrowly oblong, acute at the apex, 10–12 mm. long, 3–4 mm. broad, glabrous, the wings much narrower than the body; oil tubes solitary in the intervals, 2 on the commissure.

TYPE: *A. H. Cronquist 2856*, gravelly granitic hillside along Beaver Creek near Marsh Creek, 25 miles northwest of Stanley, Custer County, Idaho, alt. 6400 feet, July 3, 1941 (UC, TYPE; IM, MB, MINN, UIs, isotypes).

Specimens examined: IDAHO: Beneath *Pseudotsuga taxifolia* and *Pinus ponderosa* on ridge above east side of Sheep Creek, Idaho County, alt. 5500 feet, May 11, 1939, *F. G. Meyer 1614* (MEYER, UC); moist talus on hills above Sheep Creek and the Snake River Canyon, Canadian Zone, May 16, 1936, *F. G. Meyer 262a* (MEYER); Panther Creek, Lemhi County, May 16, 1941, *Ray J. Davis 3113* (UC, UIs); ½ mile below Middle Fork, Lemhi County, May 15, 1941, *Ray J. Davis 3060* (UC, UIs).

The discovery of such novelties as this bears witness to the fact that Idaho is perhaps the least fully explored of any of the continental United States. *Lomatium idahoense* appears to be most closely related to *L. laevigatum* (Nutt.) Coult. & Rose, a species of the Columbia River Valley, in Washington and Oregon. It differs, however, from *L. laevigatum* in its many fewer leaflets, fewer rays and longer and more slender fruit.

Lomatium Rollinsii Mathias & Constance, sp. nov. Plantae graciles caulescentes alterne ramosae, 2.5–5 dm. altae, e radice prima elongata saepe tuberosa, omnino crispo-puberulae; folia in ambitu oblonga, petiolo excluso 5–15 cm. longa, 3–5 cm. lata, bipinnata vel pro parte tripinnata, divisionibus ultimis linearibus acutis obtusisve, 0.2–3 cm. longis, 0.5–2 mm. latis, puberulis; petiolus basilaris, 5–15 cm. longus, ad basim anguste brevi-vaginans, caulini prorsi anguste vaginantes; involucellae bracteolae minutae filiformes; radii 4–8, adscendentes, 1.5–5 cm. longi, inaequales graciles puberuli; pedicelli filiformes, 6–15 mm. longi; umbellularum flores 8–15 lutei; fructus oblongo-ovatus, 6–7 mm. longus, 3–4 mm. latus, glaber, alis quam corpore dimidio angustioribus; vittae in intervallis dorsalibus solitariae, in lateralibus 2, in commissura 4.

Plants slender, caulescent, alternately branched, 2.5–5 dm. high, from an elongated and often tuberous taproot, crisped-puberulent throughout; leaves oblong in general outline, excluding the petiole 5–15 cm. long, 3–5 cm. broad, bipinnate or partially tripinnate, the ultimate divisions linear, acute or obtuse, 0.2–3 cm. long, 0.5–2 mm. broad, puberulent; petiole 5–15 cm. long, narrowly short-sheathing at base, those of the cauline leaves narrowly and wholly sheathing; involucel of minute, filiform bractlets; rays 4–8, ascending, 1.5–5 cm. long, unequal, slender, puberulent; pedicels filiform, 6–15 mm.

long, the umbellets 8–15 flowered; flowers yellow; fruit oblong-ovate, 6–7 mm. long, 3–4 mm. broad, glabrous, the wings one-half the width of the body; oil tubes solitary in the dorsal intervals, 2 in the lateral, 4 on the commissure.

TYPE: *Constance, Rollins & Dillon 1573*, grassy dry soil, near Deep Creek, Snake River Canyon, Wallowa County, Oregon, alt. 1000 feet, May 15, 1936 (UC, TYPE; distributed to other herbaria as *Cogswellia ambigua* (Nutt.) Jones).

Specimens examined: IDAHO: Stony soils in wheat-farming area 7 miles north of Waha, Nez Perce County, April 25, 1940, *J. H. Christ 10,877* (CHRIST, UC); on rolling hills 2 miles west of Webb, Nez Perce County, April 25, 1940, *J. H. Christ 10,889* (CHRIST, UC); on rocky hillside, Slate Creek, Salmon River Canyon, Idaho County, May 16, 1937, *J. H. Christ & W. W. Ward 7300* (CHRIST, UC), May 21, 1939, *J. H. Christ s. n.* (UC). OREGON: Basalt outcroppings on hills above the Snake River in the Snake River Canyon, Upper Sonoran Zone, Wallowa County, May 15, 1936, *F. G. Meyer 231* (MEYER).

This species adds to the growing list of plants believed to be endemic to the drainage area of the Snake and Salmon rivers. *Lomatium Rollinsii* superficially resembles *L. ambiguum* (Nutt.) Coult. & Rose, chiefly because of the mode of branching combined with the color of the flowers. The two are very probably related, but the newly detected species differs from *L. ambiguum* in being puberulent instead of glabrous, having pinnately instead of ternate-pinnately divided leaves and ovate-oblong rather than oblong fruit. The species is named for Dr. Reed C. Rollins, of Stanford University, who accompanied the junior author upon several noteworthy botanical investigations of the Snake River Canyon.

The following abbreviations for herbaria are used in this paper: Gray Herbarium, Harvard University (GH); Intermountain Herbarium, Utah State Agricultural College (IM); Missouri Botanical Garden (MB); Herbarium, University of Minnesota (MINN); University of California Herbarium, Berkeley (UC); Herbarium, University of Idaho, Southern Branch, Pocatello (UIs).

DEPARTMENT OF BOTANY, UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 61–67 JANUARY, 1943

NOMENCLATURAL CHANGES IN THE GENUS CUSCUTA, AND NOTES ON SOME AMERICAN SPECIES

T. G. YUNCKER

In volume 18 of the Memoirs of the Torrey Botanical Club, I published in 1932 a comprehensive review of all of the species of *Cuscuta* then known. Since the appearance of this paper I have examined a large number of additional specimens, some of which have proved to be new species. These have been published from time to time. Several errors, some involving rules of nomenclature, have also been discovered in the above-mentioned paper. Corrections of these errors together with the presentation of additional notes which have accumulated on a number of species are given in the following discussion.

CUSCUTA HARPERI Small, Flora S. E. U. S. ed. 2, 1361, 1913. This is one of the smallest and most inconspicuous of our American species, with flowers mostly 1 mm. or less long. It appears to enjoy a very local distribution limited to a few counties in the states of Georgia and Alabama. It was collected in Washington County, Georgia, between Peacocks and Harrison, July 20, 1906, by R M. Harper, and also 3 miles north of Harrison in the same county, June 10, 1938, by J. H. Pyron and R McVaugh (*3102*). Harper recognized the specimen he had found as probably new to science and reported it in his paper entitled "Some hitherto undescribed outcrops of Altemaha grit and their vegetation" in Torreya for December 1906. In Alabama it had been found at DeSoto Falls, Lookout Mountain, July 1898, by Albert Ruth (*773*); in the vicinity of Gadsen, Etowah County, July 29, 1900, by Pollard and Maxon (*341*); and in a rocky glade on the west side of Short Creek on Sand Mountain about 5 miles northeast of Boaz, Marshall County, August 29, 1933, by R. M. Harper (*3107*).

In each of the above specimens the host, when indentifiable, is *Chondrophora virgata* (Nutt.) Greene, with the exception of Harper's *3107* which is on *Helianthus longifolius* Pursh and *Laciniaria microcephala* Small. The host as indicated on the label for Pollard and Maxon's *341* was *Chondrophora nudata* (Michx.) Britton. In commenting on this host, however, R. M. Harper in a recent communication states "They were certainly in error in calling the host plant *Chondrophora nudata* for that species is not known outside of the coastal plain."

The type specimen for this species, as indicated by Small on page 1375 of his Flora, is the one collected by Harper in Washington County, Georgia, July 20, 1906. There are two sheets of this collection in the New York

Botanical Garden herbarium, one of which has been selected to represent the type. In error, I formerly listed Harper's *117* as the type collection.

CUSCUTA PAUCIFLORA Philippi, Linnaea **33**: 185. 1864. *C. pusilla* Philippi ex Yuncker, Mem. Torrey Club **18**: 151. 1932.

At the time the description of *C. pusilla* was published no authentic material of *C. pauciflora* had been seen, but from Philippi's original description it was decided that *C. pauciflora* was probably the same as *C. micrantha* Choisy, with which species it was questionably allied as a synonym. More recently, I. M. Johnston has loaned from Gray Herbarium a fragment of what is presumably the type of *C. pauciflora* which was collected by Philippi on *Myrtus nummularia* at Ancud, Chile, January 1858. This specimen is very fragmentary, but after carefully comparing it with the specimen upon which the description of *C. pusilla* was based, collected also by Philippi somewhat farther north at Valdivia, it now appears evident that they are the same.

C. pauciflora is distinguished with some difficulty from *C. micrantha* Choisy, another Chilean species which commonly occurs on low herbaceous hosts. The flowers of both are small, measuring about 1.5 mm. from the base up to the corolla sinuses. *C. pauciflora*, however, appears to have much longer pedicels, proportionately longer corolla lobes, more campanulate corollas, and more globose ovaries. On the basis of the specimens which have been examined *C. micrantha* also appears to have a more northern distribution.

CUSCUTA INDECORA Choisy, Mém. Soc. Phys. Hist. Nat. Genève **9**: 278. *pl. 3. f. 3.* 1841. *C. hispidula* Engelmann, Am. Jour. Sci. **45**: 75. 1843. *C. neuropetala* Engelmann, Am. Jour. Sci. **45**: 75. 1843. *C. neuropetala* Engelmann var. *littoralis* Engelmann, Bost. Jour. Nat. Hist. **5**: 223. 1845. *C. pulcherrima* Scheele, Linnaea **21**: 750. 1848. *C. decora* Englemann, Trans. Acad. St. Louis **1**: 501. 1859. *C. decora* Engelmann var. *indecora* (Choisy) Engelmann, Trans. Acad. St. Louis **1**: 502. 1859. *C. decora* Engelmann var. *pulcherrima* (Scheele) Engelmann, Trans. Acad. St. Louis **1**: 502. 1859. *C. indecora* Choisy var. *neuropetala* (Engelmann) Hitchcock, Contrib. U. S. Nat. Herb. **3**: 549. 1896.

At the time Engelmann monographed the genus *Cuscuta* (Trans. Acad. St. Louis, 1859) he replaced Choisy's earlier epithet *indecora* with his *decora* which he considered as being more appropriate, and at the same time distinguished four varieties. His variety *indecora*, which was the typical variety and the same as Choisy's species *indecora*, was characterized as having small flowers, short calyx lobes, and long pedicels. Engelmann also included under this variety a form with very hispid-papillate flowers which he had formerly described with the specific name *hispidula*.

His variety *pulcherrima* was the same as *C. neuropetala*, previously described by him together with its variety *littoralis*, and also as Scheele's

C. pulcherrima. This variety is characterized as having larger, smooth or nearly smooth flowers, with proportionately larger calyx. If this variety were to be maintained it should, according to the International Rules, retain the older epithet *littoralis* rather than the later *pulcherrima*.

I have examined many specimens of *C. indecora* collected throughout the range of the species and have found the various characters which Englemann used to distinguish variety *pulcherrima* from variety *indecora*, or the typical variety, to be exceedingly variable. The size of the flowers, the length of the pedicels and the proportionate size of the calyx vary greatly, sometimes even on the same specimen. Most of the flowers are more or less granulate because of the lenticular outer surface of the cells and occasional specimens are even papillate-hispid. There is, however, no observed constancy in the shape and degree of protrusion of the outer walls of the cells. In view of the inconstancy of any of the characters used by Engelmann to distinguish the two varieties under discussion, I have come to the conclusion that it would be better not to attempt to maintain them as separate entities.

CUSCUTA SUKSDORFII Yuncker, Mem. Torrey Club **18**: 167. f. 41. 1932.

This species was originally described from a specimen collected on *Aster* in Skamania County, Washington, in 1891 by Suksdorff (*1187*). It was also found 10 miles southeast of Port Orford, Curry County, Oregon, in 1919 by M. E. Peck (*8621*). In 1934 L. C. Wheeler collected two specimens on *Calyptridium umbellatum* above 6000 feet in the Siskiyou Mts., Siskiyou County, California (*3011; 3192*). These two specimens differed from the species in certain characters and were described as new under the varietal epithet of *subpedicellata* Yuncker (Bull. Torrey Club **62**: 512 1935). A specimen collected at Bluff Lake, at 7400 feet altitude, in the San Bernardino Mts., San Bernardino County, California, July 13, 1926, by P. A. Munz (*10678*) has recently come to my attention. In this specimen the pedicels are exceptionally long and a number of the flowers were discovered which lacked infrastamineal scales. In a few flowers, however, two or three small lateral projections representing greatly reduced scales were observed along the filament attachment line. Otherwise this plant closely resembles those from the north. This specimen from southern California may possibly represent a different variety. This can be determined, however, only upon the study of additional and more abundant material from this region. Plants of this species are inconspicuous and are to be sought at altitudes of 6000 feet or more.

CUSCUTA NEVADENSIS Johnston, Proc. Calif. Acad. IV **12**: 1133. 1924.
C. Veatchii Brandegee var. *apoda* Yuncker, Ill. Biol. Monogr. **6**: 159. 1921.
C. salina Engelmann var. *apoda* (Yuncker) Yuncker, Mem. Torrey Club **18**: 169. 1932.

Considerable trouble has been encountered in attempting to determine the correct taxonomic status of this species. I described it originally as a variety of *C. Veatchii*. Johnston later questioned its relationship to *C. Veatchii* and gave it the specific name of *C. nevadensis*. In 1932 I further complicated the nomenclature by transferring it to varietal status under *C. salina*, to which some specimens of it bear considerable resemblance. In a specimen recently studied, matured seeds were discovered for the first time. In these seeds the embryo was found to be similar to those characteristic of *C. denticulata* and *C. Veatchii*, in both of which species it exhibits an abruptly enlarged ball-like end. This character, so far known to exist only in these three species, distinguishes it from *C. salina* which possesses the more slender embryo typical of most species of *Cuscuta*. It differs from *C. Veatchii*, with which it is most likely to be confused, by having larger flowers, mostly longer pedicels, proportionately longer calyx and corolla lobes, and larger anthers on short filaments. I now agree with Johnston in considering it sufficiently different to be considered as of specific rank.

CUSCUTA GRONOVII Willdenow var. LATIFLORA Engelmann, Trans. Acad. St. Louis **1**: 508. 1859. *C. Gronovii* Willdenow var. *Saururi* (Engelmann) MacMillan, Metasp. Minn. 430. 1892.

C. Gronovii is the commonest species of dodder occurring in the central and northeastern United States and Canada. It extends southward to the gulf states, and sparingly even to the West Indies, and westward nearly to the Rocky Mountains. It does not appear to be particular as to hosts although it occurs most commonly on species, either woody or herbaceous, which grow in low, moist areas.

The specimen numbered *3160* in Willdenow's herbarium, taken as probably representing the type, has flowers which are approximately 2 mm. long from the base up to the corolla sinuses. The calyx lobes are oval-ovate, overlapping at the base and reaching to about the middle of the corolla tube which is campanulate with the sides subparallel above the center as viewed laterally. This is the variety most commonly found. The size of the flowers has been found to vary from a minimum of about 1 mm. up to 2.5 or even 3 mm. in length from the base up to the corolla sinuses. In some specimens the throat of the corolla may be narrower than the tube at the middle because of the maturing fruit; and occasional specimens may, on the contrary, exhibit somewhat funnel-form corollas. The shape of the corolla determines its position about the capsule which is commonly enveloped by the corolla when matured.

In variety *latiflora* the flowers are usually smaller. The calyx lobes are more oblong-oval and less overlapping at the base, and they reach the corolla sinuses. The corolla tube is broadly campanulate with the throat wider than

the tube which tapers towards the base. Because of its shape, the corolla is ordinarily borne at the base of the protruding, naked capsule when mature. In this variety there is also a greater tendency to produce the inflorescence endogenously. The inflorescence is also commonly more branched than for the species in general and in occasional specimens a "witches' broom" effect is produced which arouses the suspicion that there may be an unfavorable influence of the host upon the parasite.

Engelmann's varietal name *latiflora* is to be retained as valid under the International Rules. The variety occurs throughout the range of the species and appears, as in the case of the typical variety, to show no host preferences.

CUSCUTA UMBROSA Hooker, Fl. Bor. Am. **2**: 78. 1840. *C. Gronovii* Willdenow var. *curta* Engelmann, Trans. Acad. St. Louis **1**: 508. 1859. *C. megalocarpa* Rydberg, Bull. Torrey Club **28**: 501. 1901. *C. curta* (Engelmann) Rydberg, Bull. Torrey Club **40**: 466. 1913.

As has been pointed out by Engelmann, *C. umbrosa* Hooker included specimens now recognized as belonging both to *C. Gronovii* and to this species. According to Section 8, Article 52, of the International Rules, Hooker's name must be retained for one of the segregated species.

CUSCUTA COMPACTA Jussieu var. EFIMBRIATA Yuncker, Ill. Biol. Monogr. **6**: 167. 1921.

This variety, characterized by greatly reduced infrastamineal scales, was known originally only from the type specimen collected by Fredholm in Duval County, Florida. Professor Delzie Demaree found the second known specimen of it near Tillar in Desha County, Arkansas, October 24, 1936 (*11051*).

CUSCUTA GRANDIFLORA H.B.K., Nov. Gen. Sp. Pl. **3**: 123. *pl. 213.* 1818.

This is one of the most widely distributed of the South American highland species, ranging from Colombia to Chile and Argentina. It is easily recognized because of its large, attractive flowers which lack infrastamineal scales. There is considerable variation in the shape and length of the styles. Typically, the styles range up to about 1 mm. in length, are slightly flattened and taper gradually to a wider base. Occasional specimens, however, have the styles strongly flattened, and in one or two specimens examined one of the styles was found to be much longer than the other. A specimen collected by E. K. Balls in the Department of Cochabamba, Bolivia, at 11,000 feet altitude, March 15, 1939 (*6238*), has both styles much shorter than any hitherto seen for this species. The contrast is sufficiently great to suggest recognition with formal or varietal status. Because of the variation already noted in the styles of this species, however, it is believed better not to describe it as new at present from the single specimen at hand.

CUSCUTA FLOSSDORFII Hicken, Darwiniana **1**: 31. 1922. *C. brevisquamata* Yuncker, Am. Jour. Bot. **9**: 566. *pl. 1, f. 1a–e.* 1922.

This distinctive Argentina species was described under the above two names almost simultaneously in 1922. As nearly as could be determined from the original description and without having seen the type, it was decided later that *C. Flossdorfii* was closely related to *C. brevisquamata* and in 1932 I tentatively placed it as synonymous with that species.

Recently, through the kindness of Dr. Arturo Burkart, director of the Instituto de Botanica Darwinion, I have had an opportunity of examining the type of *C. Flossdorfii* and discover that it is identical with *C. brevisquamata*. I also discover that the publication of *C. Flossdorfii* occurred a short time before that of *C. brevisquamata* and, hence, has priority.

The type of *C. Flossdorfii*, now in the herbarium of the Instituto de Botanica Darwinion, was collected on *Saturcia eugenioides* by A. Flossdorf in the Province de La Rioja, Argentina, February, 1913, at 3000–4000 meters altitude. A specimen collected by Schreiter (*3057*) in the Province of Tucuman has also been seen.

CUSCUTA JAPONICA Choisy var. THYRSOIDEA Engelmann, Trans. Acad. St. Louis **1**: 517. 1859. *C. formosana* Hayata, Icon. Plant. Formos. **2**: 124. *pl. 30.* 1912. *C. japonica* Choisy var. *formosana* (Hayata) Yuncker, Mem. Torrey Club **18**: 253. 1932.

Engelmann gave the name of *thrysoidea* to variety *a* or the typical variety of *C. japonica*. Later, Hayata gave a large-flowered specimen of *C. japonica* the name of *C. formosana*. In studying *C. japonica*, I concluded that Hayata's plant differed from the typical form in certain features and decided that it should be retained as a variety. Part of the specimens listed by Engelmann as belonging to variety *thyrsoidea* also appeared to belong to the new variety as established. Thus, part of variety *thyrsoidea*, as recognized by Engelmann, remained representative of the typical variety or species and part became the variety which I listed as variety *formosana*. However, according to section 8, article 52, of the International Rules, Engelmann's earlier name should be retained for the variety rather than Hayata's later epithet.

The following nomenclatural corrections are required, for the most part, under article 58 of the International Rules:

CUSCUTA AUSTRALIS R. Brown var. **breviflora** (Visiani) Yuncker, comb. nov. *C. australis* R. Brown var. *Tinei* (Insenga) Yuncker, Mem. Torrey Club **18**: 126. 1932.

CUSCUTA RACEMOSA Martius var. MINUTA Choisy, Mém. Soc. Phys. Hist. Nat. Genève **9**: 277. 1841. *C. racemosa* Martius var. *miniata* Engelmann, Trans. Acad. St. Louis **1**: 505. 1859.

CUSCUTA REFLEXA Wallich var. BRACHYSTIGMA Engelmann, Trans. Acad.

St. Louis **1**: 519. 1859. *C. reflexa* Wallich var. *anguina* (Edgeworth) Yuncker, Mem. Torrey Club **18**: 260. 1932.

CUSCUTA CAPILLARIS Reichenbach, Icon. Bot. **5**: 64. 1827. *C. palaestina* Boissier, Diagn. Pl. Or. Nov. I. **2**[11]: 86. 1849.

CUSCUTA CAPILLARIS Reichenbach var. **syriana** (Yuncker) Yuncker comb. nov. *C. palaestina* Boissier var. *syriana* Yuncker, Mem. Torrey Club **18**: 280. 1932.

CUSCUTA EPITHYMUM Murray var. ANGUSTATA Engelmann, Trans. Acad. St. Louis **1**: 463. 1859. *C. Epithymum* Murray var. *alba* (Presl) Trabut, Bull. Soc. Bot. France **53**: xxxvii. 1907.

CUSCUTA PLANIFLORA Tenore var. **subpapillosa** (Trabut) Yuncker comb. nov. *C. planiflora* Tenore var. *Godronii* (DesMoulin) Rouy, Flore de France **10**: 359. 1908.

CUSCUTA APPROXIMATA Babington var. **Webbii** (Engelmann) Yuncker comb. nov. *C. approximata* Babington var. *Episonchum* (Webb & Berthelot) Yuncker, Mem. Torrey Club **18**: 299. 1932

In addition, errors have been detected in the form of citation of some names. These names are correctly cited as follows: *Cuscuta cordofana* (Engelmann) Yuncker, comb. nov. *Cuscuta brachycalyx* (Yuncker) Yuncker, comb. nov. *Cuscuta xanthochortos* Martius var. *carinata* (Yuncker) Yuncker, comb. nov. *Cuscuta foetida* H. B. K. var. *pycnantha* (Bentham) Yuncker *Cuscuta corymbosa* Ruiz & Pavon var. *stylosa* (Choisy) Engelmann. *Cuscuta potosina* Schaffner apud Watson. *Cuscuta potosina* Schaffner var. *globifera* Yuncker. *Cuscuta saccharata* (Engelmann) Yuncker, comb. nov *Cuscuta Epithymum* Murray var. *angustissima* (Engelmann) Yuncker, comb. nov. *Cuscuta Balansae* Boissier & Reutter ex Yuncker. *Cuscuta Balansae* Boissier & Reutter ex Yuncker var. *socotrensis* Yuncker, var. nov. *Cuscuta approximata* Babington var. *leucosphaera* (Boissier & Heldreich) Yuncker, var. nov.

I wish to thank Dr. H. W. Rickett, bibliographer of the New York Botanical Garden, for assistance in checking and verifying nomenclatural data used in the preparation of this paper.

DEPAUW UNIVERSITY
GREENCASTLE, INDIANA

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 1, pp. 68–81 JANUARY, 1943

DESCRIPTIONS OF TROPICAL RUSTS—V[1]

GEORGE B. CUMMINS

The Uredinales reported in this paper were collected, for the most part, by Paul C. Standley of the Field Museum of Natural History, during his trip to Guatemala in 1940 and 1941. He obtained 562 specimens of rusts but only those of more than ordinary interest are reported here. A few collections made by Julian A. Steyermark and John R. Johnston are also included. All specimens are from Guatemala. The type specimens are deposited in the Arthur Herbarium, Purdue University Agricultural Experiment Station. Specimens collected by Standley are also in the Field Museum of Natural History.

AECIDIUM TALINI Speg. On *Talinum triangulare* (Jacq.) Willd., Dept. SANTA ROSA: along the Avellana road south of Guazacapán, December 6, 1940, *Standley 79197*.

A portion of this collection was sent to Dr. Juan C. Lindquist who kindly compared it with material from La Viña, Salta, Argentina, which had been named by Spegazzini. He found it to agree in all respects. The species has not been reported before from North America.

AECIDIUM FUCHSIAE Jacks. & Holw. On *Fuchsia minutiflora* Hemsl., Dept. CHIMALTENANGO: Las Calderas, June 21, 1941, *Johnston 1912*.

A. fuchsiae has not been reported from North America previously and Johnston's specimen does not show complete agreement. The peridia are somewhat paler than typical and the wall of the aeciospores is thinner. For the present, however, it seems advisable to report this collection as *A. fuchsiae*.

Aecidium lycianthis Cummins, sp. nov. Pycniis non visis. Aeciis hypophyllis subepidermalibus, in maculis irregularis flavidis usque ad 2 cm. longis aggregatis, vel petiolicolis vel caulicolis, breviter cupulatis vel bullatis, pallide flavidis, 150–300 μ diam., margine lacerato vel eroso; cellulis peridii oblongis vel oblongo-ellipsoideis, 14–16 × 23–32 μ, pariete interiore verrucoso 2 μ cr., verrucis plus minusve elongatis, exteriore striato 3–3.5 μ cr.; aeciosporae ellipsoideae vel oblongae, 12–17 × 17–24 μ; membrana hyalina, 1.5–2 μ cr., minuteque verrucosa.

On *Lycianthes quichensis* (Coult. & D. Sm.) Bitter, Dept. CHIMALTENANGO: Las Calderas, November 5, 1940, *Johnston 1708*, June 21, 1941, *Johnston 1877* (TYPE); Dept. QUEZALTENANGO: Aguas Amargas, on the western slope of Volcán de Zunil, January 14, 1941, *Standley 83365*.

---

[1] Journal Paper Number 27, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany. The fourth article of this series was published in Bull. Torrey Club **68**: 467–472. 1941.

This rust is variable in habit. No hypertrophy is evident on the leaf blades but when the petioles and stems are infected there is some hypertrophy and distortion. In one specimen there are a few aecia on two flower buds, so it is not improbable that fruits may also be susceptible to infection.

There has been no previous account of a rust on *Lycianthes*.

Aecidium dahliae-maxoni Cummins, sp. nov. Pyeniis nullis. Aeciis hypophyllis, subepidermalibus, in greges 1–3 mm. diam. laxe aggregatis, sine maculis, 0.1–0.2 mm. diam., cupulatis, pallide flavidis, margine recurvato; cellulis peridii firme conjunctis, oblongis vel polyhedricis, 16–22 × 25–35 μ, pariete interiore moderate verrucoso 2–2.5 μ cr., exteriore minuteque punctato-striato 3–4 μ cr.; aeciosporae late ellipsoideae vel globoideae, 14–18 × 17–20 μ; membrana hyalina, 0.5–1 μ cr., minuteque verruculosa.

On *Dahlia maxoni* Saff., Dept. CHIMALTENANGO: Las Calderas, June 21, 1941, *Johnston 1875*.

Microscopically this species is much like *A. dahliae* Syd. but it is entirely different macroscopically because of the loosely grouped aecia. There are frequently only four or five aecia in a group and seldom more than twelve, whereas the aecia are numerous and densely grouped in Sydow's species. The absence of pycnia and the almost total absence of discoloration around the aecia provide additional differences.

ANGIOPSORA LENTICULARIS Mains On *Panicum arundinariae* Trin., Dept. CHIMALTENANGO: along Río Guacalate, southeast of Chimaltenango, December 14–23, 1940, *Standley 81037*.

Previous collections of *A. lenticularis* have all been on species of *Lasiacis*. Both uredia and telia are present in Standley's collection and both agree too well with those of *A lenticularis* to permit reference to either a new species or any other described species of *Angiopsora*. *A. lenticularis* has been collected in Guatemala on *Lasiacis*.

ANGIOPSORA PALLESCENS (Arth.) Mains. On *Euchlaena mexicana* Schrad., GUATEMALA CITY, Jardín Botánico, May 1, 1941, *Standley 92861*.

Telia are not present in this collection but the uredia and urediospores agree with those of *A. pallescens*, a species which had been collected previously only on the genus *Tripsacum*. On the basis of the relationship of the hosts one might expect that *Euchlaena* would also be susceptible to *Angiopsora zeae*.

BAEODROMUS HOLWAYI Arth. On *Senecio warscewiczii* A. Br. & Bouché, Dept. QUEZALTENANGO: region of Los Alonzo, mts. above San Juan Ostuncalco, January 21, 1941, *Standley 84176*.

This specimen, which is only scantily infected, provides the first Guatemalan record for the species. It is known otherwise only from Nevada de Toluca, Mexico, where Holway collected it on *Senecio cinerarioides* in 1903.

BUBAKIA MEXICANA Arth. On *Croton draco* Schlecht., Dept. JUTIAPA: between Jutiapa and Las Tunas, northwest of Jutiapa, November 4, 1940, *Standley 76291*; on *Croton payaquensis* Standl., Dept. JUTIAPA: vicinity of Jutiapa, October 24–November 5, 1940, *Standley 75225*.

This rust, which is characterized by the apically thickened walls of the urediospores, has not been found previously in Guatemala or on either of the above cited hosts. *B. mexicana* is known from three Mexican collections on *C. calvescens*, *C. ciliato-glandulosa* and an undetermined species.

CEROTELIUM FICI (Cast.) Arth. On *Morus insignis* Bur. ?, Dept. CHIMALTENANGO: along Río Guacalate, southeast of Chimaltenango, December 14–23, 1940, *Standley 79987*.

There has been no previous record of a rust occurring on *Morus* in North America, although *C. fici* has been collected on *Morus indica* in the Orient and on related genera of hosts in the Americas.

CHRYSOMYXA PYROLAE (DC.) Rostr. On *Pyrola secunda* var. *elatior* Lange, Dept. QUEZALTENANGO: Volcán Zunil, January 22, 1940, *Steyermark 34776*.

Since *C. pyrolae* has not before been found south of the mountains of New Mexico this collection is of more than ordinary interest from the standpoint of distribution. The collection was made at an elevation of 2500–3800 meters. Mr. Standley has informed me that *Picea*, the alternate host genus, is not present in Guatemala.

CUMMINSIELLA STANDLEYANA Cumm. On *Berberis fascicularis* (DC.), Dept. HUEHUETENANGO: Sierra de los Cuchumatanes, along road beyond La Pradera, km. 32, December 31, 1940, *Standley 81803, 81819a*.

Old aecia as well as uredia and telia are present on no. 81803 while aecia are present on no. 81819a, which was separated from no. 81819, *Puccinia berberidis-trifoliae* Diet. & Holw. None of the aecia are in good condition for study but a tentative description is presented below. There is little doubt that the aecia belong with *C. standleyana*.

Pycnia epiphyllous, subepidermal, globoid to narrowly flask-shaped, 115–135 μ wide by 140–230 μ long, reddish brown. Aecia hypophyllous, subepidermal, cupulate, 150–200 μ wide, in small groups on reddish, often somewhat hypertrophied spots up to 7 mm. in diameter, the spots falling out to leave "shot-holes"; peridium brownish, the peridial cells ellipsoid or oblong in face-view, 15–20 × 21–30 μ, the inner wall moderately rugose, 1.5 μ (?) thick, the outer wall 3–4 μ, smooth (?); aeciospores globoid or ellipsoid, 14–19 × 18–23 μ; wall hyaline, 1 μ thick, very finely verrucose.

GYMNOSPORANGIUM SPECIOSUM Peck ?. On *Juniperus mexicana* Spreng., Dept. HUEHUETENANGO: Sierra de los Cuchumatanes, along road beyond La Pradera, km. 32, December 31, 1940, *Standley 81737*.

Positive identification of this material is not possible on the basis of available material. Standley's note on the label is as follows: "Forming elongate swellings often as thick as a man's arm." Dr. Johnston, concerning what is probably the same rust, wrote (*in litt.*) as follows: "Inclosed herewith for your files is a photograph (see figure 11) of swellings on the branches of Juniperus mexicana. These swellings reach a size of 3 ft. in length and 6 in. in diameter. . . . In any case I did not get the fungus as it is out of season. Supposedly these are similar to the swellings on Cupressus but due to a distinct Gymnosporangium."

By soaking the gall collected by Standley I was able to obtain a few teliospores as well as evidence that the telia are probably cristiform, as in *G. speciosum*. The 2–4-celled teliospores are longer than typical of the species, however, since they measure 21–26 × 75–135 µ. Only remnants of the pedicels were seen and the spores were in poor condition for study. There is a definite possibility that this rust is an undescribed species but no decision can be reached until freshly sporulating galls are available.

Thus far the genus *Gymnosporangium* is represented in Guatemala only by *G. meridissimum* Crowell on *Cupressus*, *G. guatemalianum* Crowell (aecial stage only) on *Amelanchier* and by the above rust on *Juniperus*.

Kuehneola guatemalensis Cummins, sp. nov. Pycniis non visis. Aeciis uredinoidibus confluentibus in caulibus evolutis, gallas plus minusve globulosas usque ad 3 cm. diam. efformantibus, superficie flavo-brunneis; aeciosporae late ellipsoideae, ellipsoideae vel obovoideae, 19–23 × 23–32 µ; membrana 1–1.5 µ cr., minuteque echinulata, pallide aurea; poris germ. obscuris. Urediis non visis; urediosporae in telia globoideae vel late ellipsoideae, 19–25 × 23–27 µ; membrana 1 µ cr., pallide flavida vel hyalina, minuteque echinulata; poris germ. obscuris. Teliis hypophyllis, sparsis, minutis, 0.1–0.2 mm. diam., plus minus pulverulentis, pallide flavis vel albidis; teliosporae catenulatae, ex cellulis 3–8 compositis, cellulis individuis cuboideis, oblongis vel plus minusve cuneatis, ad apicem variabiliter lobatis, 18–24 µ latis, 20–30 µ altis; membrana 1–1.5 µ cr., ad apicem 2.5–5 µ cr., fere hyalina, levi; pedicello hyalino, brevi. Statim germ.

On *Rubus tuerckheimii* Rydb., Dept. GUATEMALA: slopes of Volcán de Pacaya, between San Francisco Sales and the base of the active cone, December 20, 1940, *Standley 80704*.

The teliospores of this species are apically lobed as are those of *K. arthuri* (Syd.) Jacks. but differ in having smaller cells borne in longer chains. There is no similarity in the aeciospores or urediospores of the two species.

The description of the aecia is based upon a single gall and may require revision, therefore, when future collections reveal possible variations. Aecia of *K. arthuri*, which may similarly cause large galls, show rather wide variation in habit.

Mainsia standleyi Cummins, sp. nov. (figs. 1, 2). Pycniis (fig. 1) amphigenis, intraepidermalibus, lenticularibus, 100–180 µ diam., eparaphysatis. Aeciis uredinoidibus amphigenis, maculis lenissime incrassulatis flavo-brunneis usque 8 mm. diam. occupantibus vel ad nervos lenissime incrassatos evolutis et greges elongatos formantibus, subepidermalibus, 0.1–0.3 mm. diam. vel confluentibus, flavidis, pulverulentis; paraphysibus nullis; aeciosporae (fig. 2) obovoideae vel ovoideae, 16–23 × 24–33 µ; membrana pallide flavida vel fere hyalina 2 µ cr., ad apicem 6–12 µ cr., moderate echinulata; poris germ. obscuris. Urediis aeciis conformibus (vel nullis ?). Teliis hypophyllis, inter aecia sparsis, subepidermalibus, rotundatis, 0.1–0.3 mm. diam., pulvinatis, flavo-brunneis; paraphysibus nullis; teliosporae (fig. 2) oblongae, oblongo-ellipsoideae vel ellipsoideae, ad apicem rotundatae, deorsum attenuatae, 13–19 × 28–45 µ; membrana 1.5 µ cr., ad apicem 2.5–3.5 µ cr., pallide aureo-brunnea, levi; pedicello flavidulo vel hyalino, fragili, sporam aequante vel breviore. Statim germ.

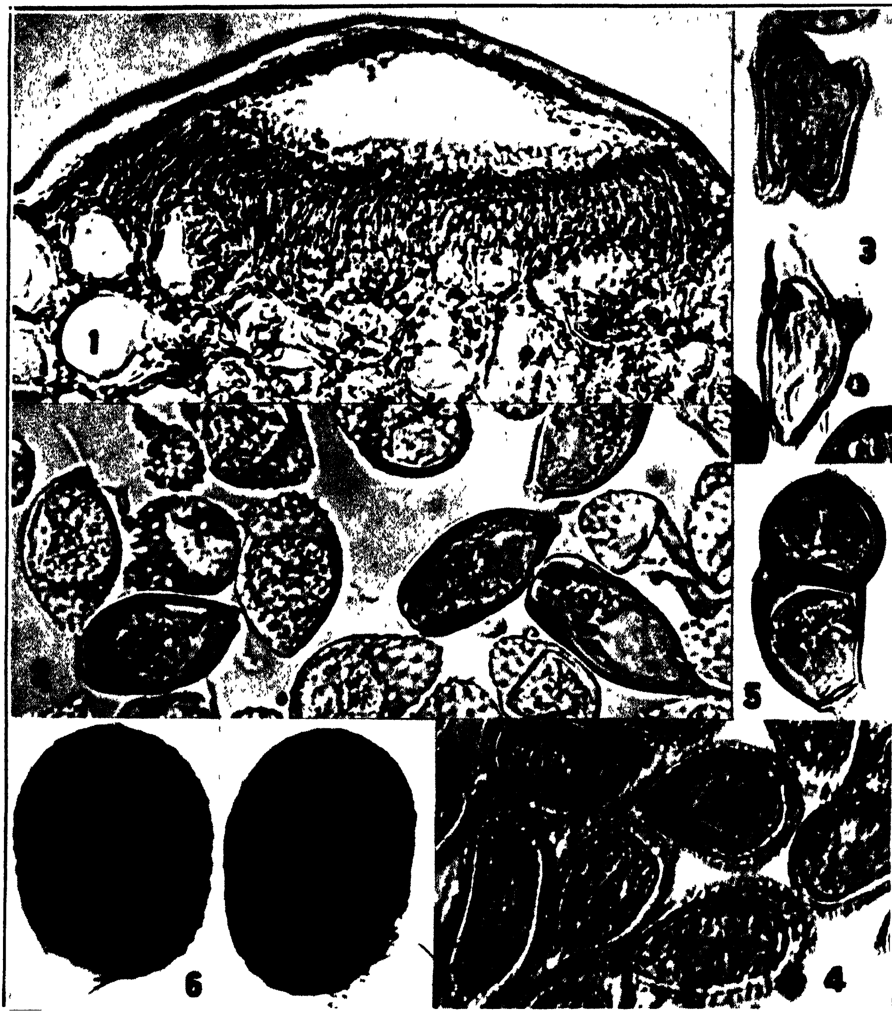


FIG. 1. *Mainsia standleyi*, freehand, unstained section of a pycnium. FIG. 2. Aeciospores and teliospores of *Mainsia standleyi*. FIG. 3. Two of the peculiar lobate urediospores characteristic of *Pileolaria standleyi*. FIG. 4. Aeciospores of *Pileolaria standleyi*; the markings tend to be longitudinally arranged. FIG. 5. One teliospore of *Puccinia degener*, a species previously known only from the uredial stage. FIG. 6. Two teliospores of *Puccinia dyschoristes*. $\times$ 800.

On *Rubus irasuensis* Liebm., Dept. ALTA VERAPAZ: damp limestone forest along the Petén highway between Campur and Socoyó, April 9, 1941, *Standley 91714.*

Mainsia standleyi differs from *M. holwayi* Jacks. in the greater apical thickening of the aeciospore wall and in the finer echinulation and from *M. peruvianum* Jacks. in having sharp round aculeae rather than longitudinally elongated markings. In addition, both *M. holwayi* and *M. peruvianum* have teliospores with uniformly thin walls.

I was unable to decide the point definitely with this material but am inclined to believe that uredia may not be formed in this species.

PHAKOPSORA VIGNAE (Bres.) Arth. On *Canavalia villosa* Benth., Dept. SACATEPÉQUEZ: along Río Guacalate, on road between Antigua and Chimaltenango, December 23, 1940, *Standley 81016*; Dept. HUEHUETENANGO: near crossing of Río San Juan Ixtán, east of San Rafael Pétzal, January 9, 1941, *Standley 83032.* On *Phaseolus macrolepis* Piper, Dept. QUEZALTENANGO: region of Las Nubes, south of San Martín Chile Verde, January 16, 1941, *Standley 83605*; along old road between Finca Pirineos and Patzulín, February 9, 1941, *Standley 86619.*

Telia, not recorded previously for this species, are present on no. 83032 and may be described as follows:

Telia hypophyllous, grouped about the uredia, blackish brown, subepidermal, crustose, 3–7 spores in thickness; teliospores variable, those in the outer layer oblong or less commonly cuboid, those in the inner layers cuboid or oblong, 6–12 × 13–23 μ; lateral walls 1 μ thick, golden or nearly hyaline, apical walls of the outermost spores 2–4 μ thick, chestnut-brown, smooth.

Hiratsuka (Bot. Mag. Tokyo **49**: 786. 1935) considers that this rust should be placed in synonymy under *Phakopsora pachyrhizi* Syd. Certainly they are similar but the teliospores described above are only about one half as large as those described by Sydow for *P. pachyrhizi* which, for the present, seems a valid reason for questioning such a treatment. Hiratsuka may be correct but until telia are found on *Vigna*, *Phaseolus*, *Eriosema*, *Dolichos* and *Teramnus* and comparative studies made it is best to accept the possibility that more than a single species may be involved.

Pileolaria standleyi Cummins, sp. nov. (figs. 3, 4). Pycniis amphigenis, in maculis purpureis 1–6 mm. diam. dense aggregatis, subcuticularibus, hemisphaericis, 50–135 μ diam. Aeciis uredinoidibus, subepidermalibus, hypophyllis, inter pycnia aggregatis, vel in petiolis et ramis junioribus deformatis dense dispositis, confluentibus, cinnamomeis, pulverulentis; aeciosporae (fig. 4) ovoideae, ellipsoideae vel oblongae, ad apicem rotundatae vel apiculatae, 16–23 × (27–) 30–35 (–37) μ; membrana cinnamomeo-bunnea, 3 μ cr., ad apicem 4–9 μ, longitudinaliter verrucosa, verrucis cuboideis vel oblongis, frequenter confluentibus; poris germ. 2 vel 3, aequatorialibus. Urediis amphigenis, subepidermalibus, sparsis, rotundatis, plus minusve pulverulentis, obscure brunneis; urediosporae (fig. 3) formam variabiles, plus minusve obovoideae, in superiore parte plerumque lobatae, rarius rotundatae, 19–26 × 28–38 μ; membrana 2 μ cr. sed ad apicem et in lobis 5–9 μ cr., cinnamomeo-brunnea, obscure longitudinaliter striata; poris germ. 2, aequatorialibus. Teliis amphigenis vel plerumque epiphyllis, subepidermalibus, in maculis purpureis 1–3 mm. diam. sparsis vel circinatis, castaneo-brunneis,

plus minusve pulverulentis; teliosporae discoideae vel globoideae, 18–26 μ alta, 24–30 μ lata; membrana 2.5–3 μ cr. vel ad apicem usque ad 4 μ cr., castaneo-brunnea, obscure rugosa vel fere levibus; poro germ. apicali; pedicello hyalino, sporam aequante.

On *Pistacia mexicana* H.B.K., Dept. BAJA VERAPAZ, rocky hills near and above Santa Rosa, in pine-oak forest, April 4, 1941, *Standley 91090*.

Pileolaria pistaciae Tai & Wei (*P. clemensiae* Cumm.), of the species which parasitize *Pistacia*, is closest to *P. standleyi* but it differs in having teliospores with longer pedicels and regularly fusiform-ellipsoid urediospores.

Few uredia are present, the infection being mainly aecial, but the peculiar lobate urediospores were seen in sufficient numbers to indicate that they are characteristic of this species and not mere abnormalities. The only other rust having similarly shaped urediospores of which I have record is *Kuehneola harrisoniae* (Syd.) Arth. & Cumm.

No previous report has been made of a *Pileolaria* on *Pistacia* in the Americas.

PROSPODIUM CONJUNCTUM (Diet. & Holw.) Cumm. On *Lippia myriocephala* S. & C., Dept. QUEZALTENANGO: along Río Samalá near Santa María de Jesús, January 25, 1941, *Standley 84636*.

This species has been collected only twice previously, on *L. pringlei* from Oaxaca, Mexico.

PUCCINIA ALIA Jacks. & Holw. On *Baccharis trinervis* (Lam.) Pers., Dept. JALAPA: vicinity of Jalapa, November 7–18, 1940, *Standley 77526*.

Since telia are not present in this collection identification cannot be positive. The aecia arise below the palisade layer and have sharply echinulate aeciospores as in *P. alia* but the spines of both aeciospores and urediospores are slightly larger than typical. *P. alia* was described from Brazil on *B. trinervis* and has not been recorded previously for North America.

PUCCINIA BERBERIDIS-TRIFOLIAE Diet. & Holw. On *Berberis fascicularis* (DC.), Dept. HUEHUETENANGO: Chémal, December 31, 1940, *Johnston 1690*; Sierra de los Cuchumatanes, along road beyond La Pradera, km. 32, December 31, 1940, *Standley 81819*.

This microcyclic species has been known previously from only the type collection made at Rio Hondo, near Mexico City.

PUCCINIA CONOCLINII Seym. (fig. 7). On *Piqueria standleyi* Rob., Dept. JUTIAPA: hills between Jutiapa and Plan de Urrutia, north of Jutiapa, October 28, 1940, *Standley 75496*.

Although this rust is common on *Ageratum*, *Conoclinium* and *Eupatorium* I can find no record of its having been collected on *Piqueria*. While differing slightly in that the teliospores tend to be narrower and commonly have the pore of the lower cell depressed the similarity is still so great that the specimen is so named with confidence.

Puccinia cuilapensis Cummins, sp. nov. (fig. 8). Pycniis et aeciis adhuc ignotis. Urediis amphigenis sed praecique hypophyllis, rotundatis, 0.1–0.3 mm. diam., flavidis, pulverulentis; urediosporae obovoideae vel late ellip-

soideae, 17–20 × 20–25 µ; membrana 1–1.5 µ cr., flavidula vel pallide aurea, moderate echinulata; poris germ. 2, aequatorialibus, obscuris. Teliis hypophyllis, rotundatis, 0.2–0.4 mm. diam., atro-brunneis, pulverulentis; teliosporae ellipsoideae, 26–30 (–32) × 37–43 (–45) µ, utrinque rotundatae, medio leniter constrictae; membrana castaneo-brunnea, 3–4 µ cr., supra poros usque ad 8 µ umbone pallidiore incrassata, moderate rugoso-verrucosa; poro superiore apicali vel plus minusve subapicali, inferiore juxta septum sito; pedicello hyalino, subpersistenti vel persistenti, plus minusve sporam aequante.

On *Salvia gracilis* Benth., Dept. QUEZALTENANGO: region of Azufral, northern slope of Volcán de Zunil, February 3, 1941, *Standley 85744*; mts. above Zunil, lower slopes of Volcán de Zunil, on road to Fuentes Georginas, February 3, 1941, *Standley 85830*. On *Salvia mocinoi* Benth., Dept. SANTA ROSA: near Cuilapa, November 20–27, 1940, *Standley 78545* (TYPE). On *Salvia* sp., Dept. SANTA ROSA: near Cuilapa, November 23, 1940, *Standley 78008*.

Only uredia are present on *Salvia gracilis* but the spores agree well with those of the type.

P. cuilapensis differs from other *Salvia* rusts having verrucose teliospores because of its yellow uredia and nearly hyaline urediospores with strictly equatorial pores. The teliospores resemble those of *P. farinacea* Long but are somewhat longer and commonly have the pore of the upper cell placed slightly to one side of the apex.

PUCCINIA DEGENER Mains & Holw (fig. 5). On *Salvia myriantha* Epling, Dept. QUEZALTENANGO: region of Las Nubes, south of San Martín Chile Verde, January 16, 1941, *Standley 83614*; vicinity of Fuentes Georginas, slopes of Volcán de Zunil, February 3, 1941, *Standley 85954*.

P. degener has been known only in the uredial stage but no. 83614 has all spore stages present, although the aecia are too old for accurate description.

Pyenia amphigenous. Aecia amphigenous, in small groups, often on veins, peridial cells collapsed but apparently mainly ellipsoid and about 21–28 × 29–35 µ, hyaline or pale yellowish, obscurely punctate; aeciospores ellipsoid, broadly ellipsoid or globoid, 17–23 × 22–27 µ, rarely larger; wall 1.5 µ thick, hyaline or yellowish, verrucose. Uredia and urediospores as described, the spores characterized by a single germpore somewhat above the hilum. Telia hypophyllous, scattered, round, 0.1–0.3 mm. diam., pulvinate, cinnamon-brown; teliospores ellipsoid or oblong-ellipsoid, (20–) 23–26 × 36–43 (–46) µ, rounded at both ends or somewhat narrowed below, moderately constricted at the septum; wall 1.5 µ thick, light cinnamon- or golden-brown, smooth; the pore in upper cell apical, next the septum in lower cell, each covered by a small conical or hemispherical, hyaline papilla 3 µ thick, the papilla disappearing at germination, which occurs without a rest period; pedicel about one-half as long as the spore or shorter, hyaline, rather fragile.

Puccinia dyschoristes Cummins, sp. nov. (fig. 6). Pyeniis et aeciis adhuc ignotis. Urediis sparsis, hypophyllis, rotundatis, 0.3–0.5 mm. diam., cinnamomeis, pulverulentis, epidermide rupta conspicue; urediosporae globoideae, late ellipsoideae vel obovoideae, 19–26 × 24–27 µ; membrana 2 µ

cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 2, aequatorialibus. Teliis amphigenis, sparsis vel aggregatis, atro-brunneis, pulverulentis, plus minusve rotundatis, usque ad 1 mm. diam., epidermide rupta conspicue; teliosporae ellipsoideae, utrinque rotundatae, ad septum non vel vix constrictae, 29–36 × 39–47 μ; membrana 4–5 μ cr., ad apicem 5–8 μ, atro-brunnea, moderate rugoso-reticulata; poro superiore apicali, inferiore prope septum vel medium loculum sito; pedicello persistenti, hyalino, sporam aequante vel longiore, deorsum rugoso.

On *Dyschoriste quadrangularis* (Oerst.) Kuntze, Dept. JUTIAPA: between Jutiapa and Las Tunas, northwest of Jutiapa, November 4, 1940, *Standley 76263*.

Puccinia dyschoristes resembles *P. ruelliae-bourgaei* Diet. & Holw. in having coarsely sculptured teliospores but differs because of the larger, thicker-walled spores. The length of the teliospores equals that of *P. longiana* but the width is greater and the wall both thicker and more coarsely sculptured. *Aecidium tracyanum* Syd. occurs on *Dyschoriste* but there is no present evidence to indicate that it belongs with *P. dyschoristes*, although the latter species is probably autoecious.

The wall of the teliospores is a deep reddish brown and bilaminate but the lamination is inconspicuous because of the density of pigmentation. The inner wall is of uniform thickness, the slight thickening over the pores being due to the outer wall, which is only slightly lighter in color. Reticulation of the surface is rather irregular and not readily discernible.

PUCCINIA FUIRENAE Cooke. On *Fuirena incompleta* Nees., Dept. HUEHUETENANGO: near crossing of Río San Juan Ixtán, east of San Rafael Pétzal, January 9, 1941, *Standley 82958*.

This appears to be the first collection of *P. fuirenae* from south of the United States.

PUCCINIA INAUDITA Jacks. & Holw. On *Wedelia acapulcensis* H.B.K., Dept. CHIMALTENANGO: Las Calderas, December 16, 1940, *Johnston 1928*; Finca La Alameda, near Chimaltenango, December 11–22, 1940, *Standley 79966*. On *Wedelia filipes* Hemsl., Dept. JALAPA: vicinity of Jalapa, November 7–18, 1940, *Standley 77531*.

These are the first collections of *P. inaudita* on the genus *Wedelia*. It has previously been recorded only on *Zexmenia*.

PUCCINIA PROBA Jacks. & Howl. On *Wedelia filipes* Hemsl., Dept. RETALHULEU: vicinity of Retalhuleu, February 17–March 1, 1941, *Standley 88747*.

Species of *Wedelia* have not been reported previously as hosts for *P. proba*.

PUCCINIA REPENTINA Jacks. & Holw. (fig. 9). On *Arracacia bracteata* C. & R., Dept. SANTA ROSA: near Cuilapa, November 20–27, 1940, *Standley 77904*.

P. repentina was described on *A. xanthoriza* Bauer from Bolivia and has not been collected previously in North America. Jackson (Mycologia **23**: 489. 1931) described the apical wall of the urediospores as 7–10 μ thick while in the Guatemalan specimen it is frequently as much as 15 μ. The

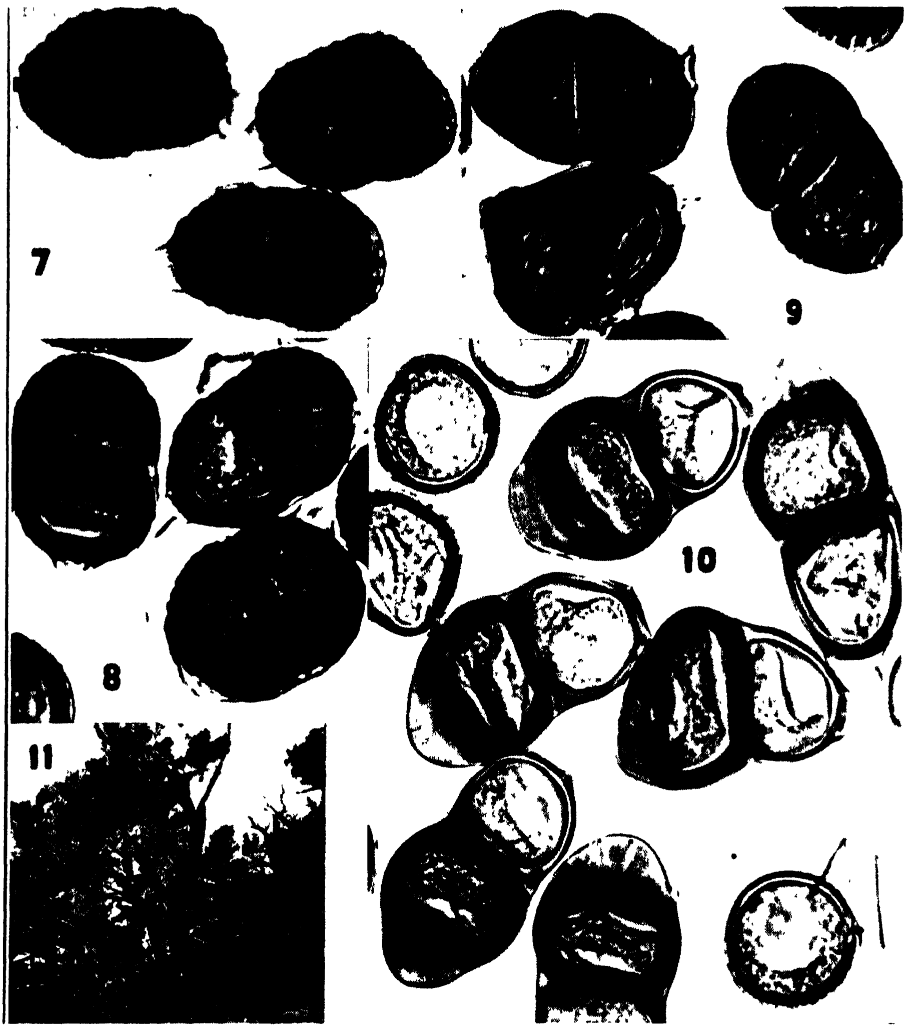


FIG. 7. *Puccinia conoclinii*; teliospores from *Piqueria standleyi*. FIG. 8. Teliospores of *Puccinia cuilapensis*. FIG. 9. Teliospores of *Puccinia repentina*, a species previously known only from South America. FIG. 10. Urediospores and teliospores of *Puccinia spegazziniana* on *Eleutheranthera ruderalis*. This rust is new to North America. × 800. FIG. 11. Photograph of a tree of *Juniperus mexicana* near Chémal. The galls are probably formed by a species of *Gymnosporangium* similar to or identical with *G. speciosum*. (Photo by Johnston, Dec. 31, 1940.)

teliospores may be verrucose, rugose or irregularly reticulate and are variable in size and shape and in the density of pigmentation. *P. arracachae* Lagerh. & Lindr. is also known to occur on this host in Guatemala.

PUCCINIA SEMOTA Jacks. & Holw. On *Hymenostephium cordatum* (H. & A.) Blake, Dept. CHIMALTENANGO: region of Los Positos, above Las Calderas, December 16, 1940, *Standley 80227, 80257.*

P. semota is known otherwise only from the type specimen on *Gymnolomia subflexuosa*, collected by Holway at Solola, Guatemala.

PUCCINIA SPEGAZZINIANA De T. (fig. 10). On *Eleutheranthera ruderalis* (Sw.) Sch. Bip., Dept. SANTA ROSA: along road southeast of Barberena, November 21, 1940, *Standley 77789.*

This rust has not been recorded previously from North America nor has it been reported on *Eleutheranthera*. However, I have compared it with a specimen collected on *Aspilia montevidensis* in Argentina by Spegazzini and can find no substantial difference. The urediospores are characteristically oblate-spheroid with a thin, cinnamon-brown wall and 3 or 4 equatorial or slightly subequatorial pores. The teliospores (fig. 10) are light chestnut- or deep golden-brown and measure 23–29 × 41–60 μ.

PUCCINIA SUBAQUILA Jacks. & Holw. On *Wedelia acapulcensis* H.B.K., Dept. JUTIAPA: vicinity of Jutiapa, October 24–November 5, 1940, *Standley 75205.*

This South American species has not been recorded previously from North America. Identification can be only tentative since teliospores are not present in this collection. The urediospores correspond, however, to those in Holway's South American material.

Ravenelia mere Cummins, sp. nov. Pycniis hypophyllis, hemisphaerico-conicis, 80–130 μ diam., subcuticularibus. Teliis amphigenis vel praecique epiphyllis, 0.5–3 mm. diam., atro-brunneis, subepidermalibus; capitulis teliosporarum convexis, atro-brunneis, levibus, 50–85 (–100) μ diam., ex sporis 4–8 in omni directione compositis; sporis individuis unicellularibus, 10–15 μ diam.; membrana 1 μ cr. flavida, ad apicem 4–6 μ cr. obscure castaneo-brunnea; cystidiis eodem numero quo cellulis marginalibus, capitulis adpressis, in aqua intumescentibus et ruptis; pedicello hyalino vel flavido, 125–200 μ longo sed deciduo, ex hyphis numerosis composito.

On *Lonchocarpus michelianus* Pittier, Dept. JUTIAPA: vicinity of Jutiapa, October 24–November 5, 1940, *Standley 75109* (TYPE). On *Lonchocarpus rugosus* Benth., Dept. RETALHULEU: San Felipe, January 13, 1917, *E. W. D. Holway 706.*

The host of the Holway specimen was originally supposed to be *Brogniartia* sp. and the rust was reported by Arthur (Am. Jour. Bot. **5**: 427. 1918) as *Ravenelia similis* (Long) Arth. Mr. Standley recently examined the host and found it to be *Lonchocarpus rugosus.*

There are two other species of *Ravenelia* on *Lonchocarpus* which may be microcyclic. One, apparently undescribed, was collected in Brazil and will probably be described by A. P. Viégas. It differs in habit and in having individual spores 22–29 μ in diameter. The other is *R. lonchocarpicola* Speg., described in 1925 (Revista Argent. Bot. **1**: 131) on *L. nitidus* in Argentina.

Through the courtesy of Dr. Lindquist I have seen this species. The teliospore-heads are slightly smaller and the individual cells 19–26 μ in diameter. The species are probably closely related.

Uredo colubrinae Cummins, sp. nov. Urediis hypophyllis, laxe aggregatis vel plus minusve aequaliter sparsis, rotundatis, 125–175 μ diam., pustulatis, subepidermalibus, diu tectis, flavidis; paraphysibus peripherales hyphoideis, incurvatis, inconspicuis, inferne conjunctis; urediosporae ellipsoideae vel obovatae, 12–17 × 18–26 μ; membrana 1 μ cr. hyalina vel pallide flavidula, subtilissime echinulata; poris germ. obscuris, verisimiliter 4, aequatorialibus.

On *Colubrina ferruginosa* Brongn., Dept. QUEZALTENANGO: below Colomba, on road toward Asintal, Feb. 20, 1941, *Standley 87894*.

When telia are discovered this species and *Uredo reissekiae* Syd. may prove to be closely related.

UREDO ERYTHRINAE P. Henn. On *Erythrina berteroana* Urban, Dept. CHIMALTENANGO: region of Los Positos, above Las Calderas, December 16, 1940, *Standley 80151;* Dept. QUEZALTENANGO: near Río Samalá, along road between Zunil and Cantel, January 18, 1941, *Standley 83940;* Dept. RETALHULEU: vicinity of Retalhuleu, February 17–March 1, 1941, *Standley 88716*.

Originally described from the Congo and known to occur also in Ceylon and the Philippines, *U. erythrinae* has been reported for the Americas only from Ecuador where Sydow collected it in 1937 on *Erythrina* sp.

UREDO FICINA Juel. On *Ficus involuta* (Liebm.) Miq., Dept. SANTA ROSA: plains north of Los Cerritos, on road between Chiquimulilla and El Ahumado, December 7, 1940, *Standley 79545*.

Uredo ficina has received varied treatment. Arthur (N. Am Flora **7**: 103. 1907) placed it in the genus *Physopella* but later (*l. c.* p. 696. 1925) included it in synonymy under *Cerotelium fici*. Sydow (Monogr. Ured. **3**: 417. 1915) listed the species as *Physopella fici*, although he did not accord *Physopella* full generic rank, and pointed out differences between it and *Kuehneola fici* (*Cerotelium fici*).

Uredo ficina differs from *C. fici* in having larger, more strongly echinulate urediospores and large, branched paraphyses. These differences are obvious and constant and until telia are found for *U. ficina* confusion can be avoided by citing it under the form-genus *Uredo*.

Uredo machaeriicola Cummins, sp. nov. Urediis praecique hypophyllis, rotundatis, 0.15–0.3 mm. diam., cinnamomeo-brunneis, sparsis vel laxe aggregatis; paraphysibus peripherales numerosis, incurvatis, cylindraceis, ad apicem acuminatis vel rotundatis, 4–7 × 40–75 μ; membrana 1.5–3 μ cr., hyalina vel flavidula; urediosporae late ellipsoideae vel obovoideae, 12–15 × 14–18 μ; membrana flavo-brunnea, minuteque echinulata, 1–1.5 μ cr.; poris germ. obscuris.

On *Machaerium biovulatum* Micheli, Dept. RETALHULEU: vicinity of Retalhuleu, February 17–March 1, 1941, *Standley 88557*.

This species differs from *U. machaerii* Diet. in having abundant paraphyses and in being foliicolous without causing hypertrophy or distortion. Its spores are of approximately the same size. *U. pusilla* Kern, Thurston & Whetzel, while having paraphyses, differs by reason of its large spores.

UREDO MUEHLENBECKIAE Jacks. & Holw. On *Muehlenbeckia tamnifolia* (H.B.K.) Meissn., Dept. QUEZALTENANGO: lower north slopes of Volcán de Santa María, above Palojunoj, January 15, 1941, *Standley 83551;* mts. southeast of Palestina, on old road to San Juan Ostuncalco, January 21, 1941, *Standley 84321.*

U. muehlenbeckiae is a new species for North America, having been recorded previously only from Ecuador and Bolivia.

Uredo obnixa Cummins, sp. nov. Uredia hypophylla, sparsa, ovoidea vel linearibus, 0.4–1.0 mm. longa, bullata, epidermide tecta, longitudinaliter dehiscentibus, cinnamomea; urediosporae obovoideae vel ellipsoideae, 17–25 × 25–33 μ; membrana 2 μ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 2, valde superaequatorialibus.

On *Cyperus melanostachyus* H.B.K., Dept. HUEHUETENANGO: about Laguna de Ocubilá, east of Huehuetenango, January 7, 1941, *Standley 82692.*

Among the *Cyperus* rusts which have superequatorial pores *P. obvoluta* Jacks. & Holw. is most like *Uredo obnixa*, but it has smaller uredia, slightly smaller and paler urediospores and pores situated nearer the equator. The spores of *U. obnixa* are also more strongly flattened and thicker-walled on the pore-bearing sides. Discovery of telia would readily decide the possible relationship with *P. obvoluta* since it has characteristic telia with stromatic paraphyses and nearly colorless teliospores with brown pedicels.

Uredo quichensis Cummins, sp. nov. Uredia epiphylla, subcuticularia, sparsa, rotundata, 0.1–0.2 mm. diam., flavo-brunnea; paraphysibus copiosis, capitatis, 10–16 × 40–65 μ, membrana 1 μ cr., hyalina vel ad apicem 1.5–2 μ cr. et aureo-brunnea; urediosporae ellipsoideae vel oblongo-ellipsoideae, 16–19 × 25–30 μ; membrana 1.5–2 μ cr. vel ad apicem et basim usque ad 3 μ cr., cinnamomeo-brunnea, dense echinulato-verrucosa; poris germ. 8–10 bizonatis instructis.

On *Calliandra conzattiana* (B. & R.), Dept. EL QUICHÉ, oak forest along road to Aguacatán, near the boundary of Dept. Huehuetenango, December 27, 1940, *Standley 81393.*

Uredo quichensis differs from *Ravenelia bizonata* Arth. & Holw. in having paraphyses with a thin apical wall and larger, uniformly and more coarsely sculptured urediospores whose wall is thicker. The species undoubtedly will prove to be a *Ravenelia.*

Uromyces calopogonii Cummins, sp. nov. Uredia subepidermalia, hypophylla, pulverulenta, cinnamomeo-brunnea, rotundata, 0.2–0.3 mm. diam.; urediosporae globoideae vel late ellipsoideae, 15–17 × 16–19 μ; membrana 1–1.5 μ cr., minuteque echinulata, pallide cinnamomeo-brunnea; poris germ. 4, aequatorialibus. Telia uredia conformibus sed castaneo-brunnea; teliosporae late ellipsoideae, ovoideae vel obovoideae, utrinque rotundatae vel deorsum plus minusve attenuatae, 13–16 × 16–19 μ; membrana pallide castaneo-brunnea, minuteque verrucosa, 1.5–2 μ cr., ad apicem 2.5–3 μ cr.; pedicello hyalino, brevi, fragili.

On *Calopogonium galactioides* (H.B.K.) Benth., Dept. CHIMALTENANGO: Finca La Alameda, near Chimaltenango, October 26, 1936, *Johnston 165;* December 11–22, 1940, *Standley 79808* (TYPE); between Chimaltenango and San Martín Jilotepeque, December 22, 1940, *Standley 80947.*

Calopogonium has not been reported previously as a host for species of the Uredinales. *U. calopogonii* is notable for its small urediospores and teliospores.

UROMYCES SCLERIAE P. Henn. On *Scleria bracteata* Cav., Dept. ALTA VERAPAZ: Finca Samac, northwest of Cobán, March 23, 1941, *Standley 89700*.

This species, originally described from South America, has not been recorded previously for Central America. Both uredia and telia are present, the urediospores characteristic because of the apically thickened wall.

Uropyxis diphysae (Arth.) Cummins, comb. nov. (*Calliospora diphysae* Arth., Bot. Gaz. **39**: 391. 1905.) On *Diphysa floribunda* Peyr., Dept. HUEHUETENANGO: near crossing of Río San Juan Ixtán, east of San Rafael Pétzal, January 9, 1941, *Standley 82872*.

This species has apparently never been transferred to *Uropyxis*, although *Calliospora* is no longer recognized as a valid genus.

THE ARTHUR HERBARIUM, PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION
LAFAYETTE, INDIANA

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

The Index to American Botanical Literature is classified under 8 headings as follows: Plant Taxonomy and Floristics (exclusive of fungi); Morphology (including anatomy, and cytology in part); Plant Physiology; Mycology and Phytopathology; Genetics (including cytogenetics); Paleobotany; Ecology and Plant Geography; General Botany (including biography). It is realized that some articles do not fall readily in any of these classifications, and users of the Index interested in a particular topic are requested to examine also classifications which may include closely related topics.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)
(See also Ecology and Plant Geography: **Camp**)

Allen, C. K. Studies in the Lauraceae, V. Some eastern Asiatic species of *Beilschmiedia* and related genera. Jour. Arnold Arb. **23:** 444–463. O 1942.

Baird, V. B. Wild violets of North America. 1–225 p. *pl. 1–77.* Univ. California Press, Berkeley, 1942.

Balls, E. K. Central and South American potatoes for the improvement of European and North American stocks. Proc. 8th Am. Sci. Cong. **3:** 143–147. 1942.

Barkley, F. A. A key to the genera of the Anacardiaceae. Am. Midl. Nat. **28:** 465–474. S 1942.

Beetle, A. A. Studies in the genus *Scirpus* L. V. Notes on the section *Actaeogeton* Reich. Am. Jour. Bot. **29:** 653–656. O 1942.

Boivin, B. Notes sur quelques introductions récentes dans le Québec. Nat. Canad. **69:** 206, 207. A–S 1942.

Brown, W. V. *Panicum bennettense*, a new species from North Carolina. Bull. Torrey Club **69:** 539, 540. *f. 1.* 3 O 1942.

Burkart, A. Los frutos de las especies silvestris de *Arachis*. Proc. 8th Am. Sci. Cong. **3:** 175–178. *f. 1.* 1942.

Burns, G. W. The taxonomy and cytology of *Saxifraga pensylvanica* L. and related forms. Am. Midl. Nat. **28:** 127–163. *f. 1–13.* Jl 1942.

Camargo, F. C. Pesquisas taxonômicas sôbre os gêneros *Pseudananas* e *Ananas*. Proc. 8th Am. Sci. Cong. **3:** 179–192. *pl. 1–3.* 1942.

Camp, W. H. On the structure of populations in the genus *Vaccinium*. Brittonia **4:** 189–204. 7 O 1942.

Camp, W. H. A survey of the American species of *Vaccinium*, subgenus *Euvaccinium*. Brittonia **4:** 205–247. 7 O 1942.

Chardon, C. E. Regarding the botanical classification of the "Chaguaramo" or Venezuelan Royal Palm. Proc. 8th Am. Sci. Cong. **3:** 195. 1942.

Chrysler, M. A. An unusual *Botrychium*. Am. Fern Jour. **32:** 87–89. *1 f.* Jl–S 1942.

Clausen, R. T. *Ophioglossum vulgatum* on the inner Coastal Plain of Alabama. Am. Fern Jour. **32:** 105–108. Jl–S 1942.

Conzatti, C. El origen probable de las Monocotiledóneas. Proc. 8th Am. Sci. Cong. **3:** 197. 1942.

Couch, G. C. The algae of the Boston Mountain region of Arkansas. Abst. Doct. Dissert. Ohio State Univ. **38:** 39–45. 1942.

Croizat, L. Amoenitates cactologicae. II. Desert **14:** 134–136. S 1942.

Croizat, L. *Haageocereus* Backeberg (Syn.: *Binghamia* Britton and Rose p.p.). Cactus & Succ. Jour. **14:** 145–148. O–N 1942.

Croizat, L. New and critical Euphorbiaceae from the tropical Far East. Jour. Arnold Arb. **23:** 495–508. O 1942.

Cuatrecasas, J. Cucurbitaceae novae Colombianae—I. Caldasia 5: 21–28. 1 Au 1942.

Cuatrecasas, J. Estudios sobre plantas Andinas, III. Caldasia 5: 17, 18. *1 pl.* 1 Au 1942.

Davis, R. J. *Geum triflorum* Pursh. Rhodora **44:** 405, 406. 17 O 1942.

Deam, C. C. *et al.* Indiana plant distribution records, II. 1941. Proc. Ind. Acad. **51:** 120–129. Je 1942.

Dugand, A. Dos adiciones a las especies nuevas Colombianas del genero *Ficus*. Caldasia **5:** 37–39. 1 Au 1942.

Dugand, A. Dos nuevas Bignoniaceas del Valle de Magdalena. Caldasia 5: 29–35. *f. 1.* 1 Au 1942

Dugand, A. Nota adicional sobre *Mauritia minor* Burret. Caldasia 5: 40. 1 Au 1942.

Erickson, R. O. The type of *Clematis hirsutissima*. Madroño **6:** 259, 260. 23 O 1942.

Ewan, J. Annotations on West American ferns—II Am. Fern Jour. **32:** 90–104 *pl. 10.* Jl–S 1942

Fernald, M. L. *Ranunculus abortivus* L., forma *coptidifolius*, forma nova. Rhodora **44:** 408 17 O 1942

Fosberg, F. R. *Cornus sericea* L. (*C. stolonifera* Michx.). Bull. Torrey Club **69:** 583–589. 2 N 1942

Fosberg, F. R. The genus *Batocarpus* Karst (Moraceae). Proc. Biol. Soc. Wash. **55:** 99–102. 13 Au 1942.

Foster, A. S. & San Pedro, M. R. Field studies on *Microcycas calocoma*. Mem. Soc. Cubana Hist. Nat. **16:** 105–131 *pl. 10–17.* Au 1942.

Fulford, M. & Shacklette, H. T. A list of Kentucky mosses. Bryologist **45:** 125–134. O 1942.

Grover, F. O. Phyllotaxy of *Catalpa*. Rhodora **44:** 414–416. N 1942.

Guard, A. T. & Silver, W. H. A new station for *Orobanche ludoviciana*. Proc. Ind. Acad. **51:** 116, 117. *1 f.* Je 1942.

Haupt, A. W. Notes on some Hepaticae of Costa Rica. Bryologist **45:** 138–146. O 1942.

Hollenberg, G. J. Phycological notes—I. Bull. Torrey Club **69:** 528–538. *f. 1–14.* 3 O 1942.

Holmgren, A. H. A rare *Selaginella* from northeastern Nevada. Am. Fern Jour. **32:** 86, 87. Jl–S 1942.

Howard, R. A. Studies of the Icacinaceae, III. A revision of *Emmotum*. Jour. Arnold Arb. **23:** 479–494. *pl. 1–4.* O 1942.

Hull, E. D. *Euphorbia Geyeri* in Indiana. Rhodora **44:** 407, 408. 17 O 1942.

Jones, C. H. Additions to the revised catalogue of Ohio vascular plants. X. Ohio Jour. Sci. **42:** 201–210. S 1942.

Kobuski, C. E. Studies in the Theaceae, XIII. Notes on the Mexican and Central American species of *Ternstroemia*. Jour. Arnold Arb. **23:** 464–478. O 1942.

Krukoff, B. A. & Monachino, J. The American species of *Strychnos*. Brittonia **4:** 248–322. 7 O 1942.

Li, Hui-Lin The Araliaceae of China. Sargentia **2:** 1–134. f. 1–14. 26 O 1942.

Lindsay, G. A new variety of *Ferocactus alamosanus*. Cactus & Succ. Jour. **14:** 139–143. *f. 83–89.* O–N 1942.

Little, E. L. Liverworts at Rainbow Bridge National Monument, Utah. Bryologist **25:** 148, 149. O 1942.

Little, E. L. Notes on the genus *Riccia* in New Mexico. Bryologist **45:** 147, 148. O 1942.

Lundell, C. L. Flora of eastern Tabasco and adjacent Mexican areas. Contr. Univ. Mich. Herb. **8:** 5–74. *f. 1–7.* S 1942.

Lundell, C. L. Studies of American Spermatophytes—III. Plants of Texas, Chiapas, and British Honduras. Contr. Univ. Mich. Herb. **8:** 75–88. *pl. 1–4.* S 1942.

McVaugh, R. Rosaceae of Nevada. *In* Contributions toward a flora of Nevada No. 22. U. S. Dept. Agr. Div. Plant Exploration. Bur. Plant Ind. 100 mimeographed pages. 15 Je 1942.

Mangelsdorf, P. C. The origin of maize. Proc. 8th Am. Sci. Cong. **3:** 267–271. 1942.

Merrill, E. D. A generally overlooked Rafinesque paper. Proc. Am. Philos. Soc. **86:** 72–90. 25 S 1942.

Moran, R. Delimination of genera and subfamilies in the Crassulaceae Desert **14:** 125–128. S 1942.

Muller, C. H. The Central American species of *Quercus*. U. S. Dept. Agr. Misc. Publ. 477: 1–216. *pl. 1–124.* Jl 1942.

Ogden, E. C. New range records for linear-leaved species of *Potamogeton*. Rhodora **44:** 406, 407. 17 O 1942.

Papenfuss, G. F. Notes on algal nomenclature: I *Pollexfenia*, *Jeannerettia* and *Mesotrema*. Proc. Nat. Acad. **28:** 446–451. O 1942.

Parker, D. Additions to the Hepaticae of Indiana. I. Proc. Ind. Acad. **51:** 100–102. Je 1942.

Pierce, J. H. A new *Dussia* and *Ormosia avilensis*. Bull Torrey Club **69:** 190, 191. N 1942.

Porter, C. L. A spring flora of the Laramie area. Rocky Mt. Herb. Leafl. **1:** 1–37. *f. 1–34.* mimeographed 1942.

Porter, C. L. Studies in Wyoming grasses. IV. Tribe Hordeae, the barley grasses. Univ. Wyoming Publ. **9:** 17–31. 31 Au 1942.

Schultes, R. E. Plantae Colombianae II. Yoco: A stimulant of southern Colombia. Bot. Mus. Leafl. **10:** 301–324. *pl. 28, 29.* 30 O 1942.

Smith, A. C. Studies of Papuasian plants, V. Jour. Arnold Arb. **23:** 417–443. O 1942.

Smith, G. M. Notes on some brown algae from the Monterey Peninsula, California. Am. Jour. Bot. **29:** 645–653. *f. 1–13.* O 1942.

Smith, L. B. Bromeliaceas notables de Colombia—II. Caldasia **5:** 5–10. *f. 1–5.* 1 Au 1942.

Summerhayes, V. S. African orchids. XII. Bot. Mus. Leafl. **10:** 257–299. 9 O 1942.

Svihla, R. D. Some Marchantiales from Mexico, Costa Rica and Panama. Bryologist **45:** 135–137. O 1942.

Sweet, J. Florida native orchids in bloom. Am. Orchid Soc. Bull. **11:** 152. *illustr.* 1 O 1942.

Tolstead, W. L. New and noteworthy records of the flora of Nebraska. Am. Midl. Nat. **28:** 482–485. S 1942.

Tolstead, W. L. A note on unusual plants in the flora of northwestern Nebraska. Am. Midl. Nat. **28:** 475–481. S 1942.

Tryon, R. M. A new *Dryopteris* hybrid. Am. Fern Jour. **32:** 81–85. *pl. 8–9.* Jl–S 1942.

Tseng, C. K. & Gilbert, W. J. On new algae of the genus *Codium* from the South China Sea. Jour. Wash. Acad. **32:** 291–296. *f. 1–3.* 15 O 1942.

Van Dersal, W. R. Ornamental American shrubs. xii, 1–288 p. *pl. 1–68 + 1 col.* Oxford Univ. Press, New York. 1942.

Turrill, W. B. Taxonomy and phylogeny. Bot. Rev. **8:** 473–532. O 1942.

Waters, C. E. Proliferous Scott's spleenwort. Am. Fern Jour. **32:** 109–111. Jl–S 1942.

Welch, W. H. Studies in Indiana Bryophytes IV. Proc. Ind. Acad. **51:** 103–113. *f. 1–31.* Je 1942.

Wherry, E. T. *Lycopodium sabinaefolium* in Pennsylvania. Am. Fern Jour. **32:** 111–113. Jl–S 1942.

Williams, L. O. Algunas orquidaceas Americanas. Caldasia **5:** 11–16. *f. 1.* 1 Au 1942.

Williams, L. O. A new *Gastrodia* from Netherlands New Guinea. Am. Orchid Soc. Bull. **11:** 210. *pl. 6.* 1 N 1942.

Williams, L. O. Two new species of *Pleurothallis* from Mexico. Am. Orchid Soc. Bull. **11:** 166–168. *pl. 5.* 1 O 1942.

Yuncker, T. G. Three new *Cuscutas* from Western North America. Bull. Torrey Club **69:** 541–543. *f. 1, 2.* 3 O 1942

MORPHOLOGY

(including anatomy, and cytology in part)

(See also under Mycology and Phytopathology **Cutter;** under General Botany **Gustafson**)

Bannan, M. W. Notes on the origin of adventitious roots in the native Ontario conifers. Am. Jour. Bot. **29:** 593–598. *f. 1–17.* O 1942.

Castle, E. S. Spiral growth and reversal of spiraling in *Phycomyces*, and their bearing on primary wall structure Am. Jour. Bot. **29:** 664–672. *f. 1–10.* O 1942.

Cave, M. S. Development of the macrogametophyte on *Miersia chilensis.* Bot. Gaz. **104:** 185–187. *f. 1–10.* 12 O 1942.

Cooper, G. O. Microsporogenesis and development of seed in *Lobelia cardinalis.* Bot. Gaz. **104:** 72–81. *f. 1–40.* 12 O 1942.

Knowlton, C. H. Fasciation in *Lilium canadense.* Rhodora **44:** 407. 17 O 1942.

Matzke, E. B. & Hulbary, R. L. An analysis of the wood of the three commercial species of white pine. Bull. Torrey Club **69:** 573–582. *f. 1–5.* N 1942.

Patterson, M. T. Cytology of apogamy in *Polystichum tsussemense.* Bot. Gaz. **104:** 107–114. *f. 1–9.* 12 O 1942.

Reynolds, M. E. Development of the node in *Ricinus communis.* Bot. Gaz. **104:** 167–170. *f. 1–9.* 12 O 1942.

Riley, H. P. & Morrow, D. Cell size in developing ovaries of *Iris fulva.* Bot. Gaz. **104:** 90–98. *f. 1–7.* 12 O 1942.

Smith, F. H. Development of the gametophytes and fertilization in *Camassia.* Am. Jour. Bot. **29:** 657–663. *f. 1–30.* O 1942.

Tukey, H. B. & Young, T .O. Gross morphology and histology of developing fruit of the apple. Bot. Gaz. **104:** 3–25. *f. 1–69.* 12 O 1942.

PLANT PHYSIOLOGY

(See also under General Botany: **Gustafson**)

Allison, F. E., Hoover, S. R. & Minor, F. W. Biochemical nitrogen fixation studies. IV. Experiments with excised legume nodules. Bot. Gaz. 104: 63–71. 12 O 1942.

Avery, G. S. Growth. Ann. Rev. Phys. **4:** 115–138. 1942.

Avery, G. S., Berger, J. & Shalucha, B. Total auxin extraction from wheat. Am. Jour. Bot. **29:** 612–616. O 1942.

Bausor, S. C. Effects of growth substance in reserve starch. Bot. Gaz. **104:** 115–121. *f. 1–8.* 12 O 1942.

Bensley, R. R. Chemical structure of cytoplasm. Science **96:** 389–393. 30 O 1942.

Burkholder, P. R. & McVeigh, I. The increase of B vitamins in germinating seeds. Proc. Nat. Acad. 28: 440–446. O 1942.

Comar, C. L. Chloroplast substance of spinach leaves. Bot. Gaz. **104:** 122–127. 12 O 1942.

Cornman, I. Susceptibility of *Colchicum* and *Chlamydomonas* to colchicine. Bot. Gaz. **104:** 50–62. *f. 1–8.* 12 O 1942.

Eaton, S. V. Volatile sulphur content of black mustard plants. Bot. Gaz. **104:** 82–89. 12 O 1942.

Eigsti, O. J. A cytological investigation of *Polygonatum* using the colchicine pollen tube technique. Am. Jour. Bot. **29:** 626–636. *f. 1–18.* O 1942.

Flint, L. H. Note on phototropism in *Pilobolus.* Am. Jour. Bot. **29:** 672–674. *f. 1.* O 1942.

Girton, R. E. & Park, E. R. Respiration studies on germinating white oak acorns. Proc. Ind. Acad. **51:** 83–86. Je 1942.

Hamner, C. L. Effects of platinum chloride on bean and tomato. Bot. Gaz. **104:** 161–166. *f. 1–2.* 12 O 1942.

Herrick, J. A. & Alexopoulos, C. J. Thiamine production by *Actinomyces viridochromogenus.* Bull. Torrey Club **69:** 569–572. N 1942.

Huffaker, C. B. Vegetational correlations with vapor pressure deficit and relative humidity. Am. Midl. Nat. **28:** 486–500. S 1942.

Inman, O. L. What the study of the green plant has taught us concerning a mechanism of photosynthesis. Proc. 8th Am. Sci. Cong. **3:** 239–242. 1942.

Karling, J. S. The response of *Achras zapota* in latex yield to wounding by the ibidem method of tapping. Bull. Torrey Club **69:** 553–560. *f. 1–4.* N 1942.

Marth, P. C. Effects of growth-regulating substances on shoot development of roses during common storage. Bot. Gaz. **104:** 26–49. *f. 1–11.* 12 O 1942.

Meyer, S. L. Physiological studies on mosses. IV. Regeneration in *Physcomitrium turbinatum.* Bot. Gaz. **104:** 128–132. *f. 1–16.* 12 O 1942.

Mullison, W. R. Certain aspects of the nutrition of tomato seedlings in sand culture. Proc. Ind. Acad. **51:** 94–99. *f. 1–3.* Je 1942.

Nielsen, C. S. Effects of photoperiod on microsporogenesis in Biloxi soybean. Bot. Gaz. **104:** 99–106. *f. 1–19.* 12 O 1942.

Overbeek, J. van Water uptake by excised root systems of the tomato due to non-osmotic forces. Am. Jour. Bot. **29:** 677–683. O 1942.

Reid, M. E. Variations in ascorbic acid and dry matter content of cowpea plants at different times of day. Bull. Torrey Club **69:** 522–527. 3 O 1942.

Robbins, W. J. A pyrimidine analog of thiamine and the growth of fungi. Proc. Nat. Acad. **28:** 352–355. S 1942.

Robbins, W. J. Vitamins as growth substances for plants. Proc. 8th Am. Sci. Cong. **3:** 277, 278. 1942.

Robbins, W. J. & Ma, R. Pimelic acid, biotin and certain fungi. Science **96:** 406, 407. 30 O 1942.

Robbins, W. J., Mackinnon, J. E., & Ma, R. Vitamin deficiencies of *Trichophyton discoides.* Bull. Torrey Club **69:** 509–521. *f. 1–3.* 3 O 1942.

Rohrbaugh, L. M. Effects of light quality on growth and mineral nutrition of bean. Bot. Gaz. **104:** 133–151. *f. 1–9.* 12 O 1942.

Schroeder, R. A. & Albrecht, W. A. Plant nutrition and the hydrogen ion—III. Soil calcium and the oxalate content of spinach. Bull. Torrey Club **69:** 561–568. *f. 1–4.* N 1942.

Thimann, K. V., Skoog, F. & Byer, A. C. The extraction of auxin from plant tissues. II. Am. Jour Bot. **29:** 598–606. *f. 1–4.* O 1942.

GENETICS

(including cytogenetics)

Blakeslee, A. F. Induced evolution in plants through chromosome changes. Proc. 8th Am. Sci. Cong. **3:** 173. 1942.

Dodge, B. O. Genetic interpretations of cultural variations in the fungi. Proc. 8th Am. Sci. Cong. **3:** 199–206. 1942.

Giles, N. H. Autopolyploidy and geographical distribution in *Cuthbertia graminea* Small. Am. Jour. Bot. **29:** 637–645. *f. 1–5.* O 1942.

Goodspeed, T. H. Experimental induction of heritable and other alterations in the fungus *Neurospora tetrasperma.* Proc. 8th. Am. Sci. Cong. **3:** 223–229. 1942.

Goodspeed, T. H. The South American genetic groups of the genus *Nicotiana* and their distribution. Proc. 8th Am. Sci. Cong. **3:** 231–238. 1942.

Graves, A. H. Breeding work toward the development of a timber type of blight-resistant chestnut: report for 1941. Am. Jour. Bot. **29:** 622–626. *f. 1–3.* O 1942

Greenleaf, W. H. Genetic sterility in *Tabacum*-like amphidiploids of *Nicotiana.* Jour. Genetics. **43:** 69–96 *pl. 3–6 + f. 1–21.* Ja 1942.

Hecht, A. Colchicine induced tetraploidy in *Oenothera.* Proc. Ind. Acad. **51:** 87–93. *pl. 1.* Je 1942.

Kearney, T. H. Cotton breeding in relation to taxonomy. Proc. 8th Am. Sci. Cong. **3:** 251–255. 1942.

Murneek, A. E. & Wittwer, S. E. Relation of sexual reproduction to development of horticultural plants I, II. Proc. Am. Soc. Hort. Sci. **40:** 201–208. My 1942.

Myers, W. M. & Hill, H. D. Variations in chromosomal association and behavior during meiosis among plants from open-pollinated populations of *Dactylis glomerata.* Bot. Gaz. **104:** 171–177. 12 O 1942.

Richey, F. D. Mock-dominance and hybrid vigor. Science **96:** 280, 281. 18 S 1942.

Stebbins, G. L. The genetic approach to problems of rare and endemic species. Madroño **6**: 241–258. *f. 1–2.* 23 O 1942.

Stout, A. B. & Chandler, C. Hereditary transmission of induced tetraploidy and compatibility in fertilization. Science **96**: 257, 258. 11 S 1942.

MYCOLOGY AND PHYTOPATHOLOGY

(See also under Morphology: **Castle;** under Genetics: **Dodge; Goodspeed**)

Alexander, L. J. A new strain of the tomato leaf-mold fungus (*Cladosporium fulvum*). Phytopathology **32**: 901–904. *f. 1.* O 1942.

Barghoorn, E. S. The occurrence and significance of marine cellulose-destroying fungi. Science **96**: 358, 359. 16 O 1942.

Bitancourt, A. A. & Jenkins, A. E. New discoveries of Myriangiales in the Americas. Proc. 8th Am. Sci. Cong. **3**: 149–172. *pl. 8–10.* 1942.

Braun, A. E. Resistance of watermelon to the wilt disease. Am. Jour. Bot. **29**: 683, 684. O 1942.

Carpenter, J. B. Moldy core of apples in Wisconsin. Phytopathology **32**: 896–900. O 1942.

Cooley, J. S. Defoliation of American holly cuttings by *Rhizoctonia.* Phytopathology **32**: 905–909. *f. 1, 2.* O 1942.

Cutter, V. M. Nuclear behavior in the Mucorales—I. The *Mucor* pattern. Bull. Torrey Club **69**: 480–508. *f. 1–66.* 3 O 1942. II. The *Rhizopus, Phycomyces* and *Sporodinia* patterns. 592–616. *f. 1–21.* N 1942.

Fitzpatrick, H. M. Revisionary studies in the Coryneliaceae. II. The genus *Caliciopsis.* Mycologia **34**: 489–514. *f. 1–35.* 1 O 1942.

Goss, R. W. & Jensen, J. H. Susceptibility of *Solanum* species to *Fusarium solani* var. *eumartii.* Phytopathology **32**: 913. O 1942.

Hagelstein, R. A new genus of the Mycetozoa. Mycologia **34**: 592, 593. O 1942.

Hills, C. H. & McKinney, H. H. The effect of mosaic virus infetion on the protein content of susceptible and resistant strains of tobacco. Phytopathology **32**: 857–866. O 1942.

Honey, E. E. *Monilinia amelanchieris.* Mycologia **34**: 575–578. 1 O 1942.

Johnston, J. R. Diseases and insect pests of pine trees in Guatemala. Proc. 8th Am. Sci. Cong. **3**: 245–250. 1942.

Karling, J. S. A new chytrid with giant zoospores: *Septochytrium macrosporum* sp. nov. Am. Jour. Bot. **29**: 616–622. *f. 1–15.* O 1942.

Lackey, C. F. Relative concentrations of two strains of curly-top virus in tissues of susceptible and resistant beans. Phytopathology **32**: 910–912. O 1942.

Linder, D. H. A contribution towards a monograph of the genus *Oidium* (Fungi imperfecti). Lloydia **5**: 165–207. S 1942.

Lohman, M. L., Cash, E. K. & Davidson, R. W. An undescribed *Atropellis* on cankered *Pinus virginiana.* Jour. Wash. Acad. **32**: 296–298. *f. 1.* 15 O 1942.

Long, W. H. Studies in the *Gasteromycetes* VI. Mycologia **34**: 532–535. 1 O 1942.

Miles, L. E. & Epps, J. M. The downy mildew disease of oats, caused by *Sclerospora macrospora.* Phytopathology **32**: 867–878. *f. 1, 2.* O 1942.

Murrill, W. A. Florida resupinate polypores. Mycologia **34**: 595, 596. 1 O 1942.

Pryor, D. E. The influence of vitamin B_1 on the development of cantaloupe powdery mildew. Phytopathology **32**: 885–895. O 1942.

Ray, W. W. Notes on Oklahoma Cercosporae—II. Mycologia **34**: 558–562. 1 O 1942.

Rea, P. M. Fungi of southern California. I. Mycologia **34**: 563–574. *f. 1–3.* 1 O 1942.

Routien, J. B. Notes on fungi previously unreported from Missouri. Mycologia **34:** 579–583. 1 O 1942.

Sakr, El Sayed, & Thompson, H. C. Effect of infecting carrot plants with certain viruses on seedstalk development. Plant Physiol. **17:** 500–502. *f. 1.* Jl 1942.

Salvin, S. B. Preliminary report on the intergeneric mating of *Thraustotheca clavata* and *Achlya flagellata.* Am. Jour. Bot. **29:** 674–676. *f. 1, 2.* O 1942.

Seaver, F. J. & Waterston, J. M. Contributions to the mycoflora of Bermuda —III. Mycologia **34:** 515–524. *f. 1–3.* 1 O 1942.

Shanor, L. & Olive, L. S. Notes on *Araiospora streptandra.* Mycologia **34:** 536–542. *f. 1–11.* 1 O 1942.

Verrall, A. F. A comparison of *Diplodia natalensis* from stained wood and other sources. Phytopathology **32:** 879–884. O 1942.

Whetzel, H. H. *Ciliospora albida.* Mycologia **34:** 525–531. *f. 1.* 1 O 1942.

Whetzel, H. H. A new genus and new species of brown-spored inoperculate discomycetes from Panama. Mycologia **34:** 584–591. *f. 1–5.* 1 O 1942.

Whiffen, A. J. A discussion of some species of *Olpidiopsis* and *Pseudolpidium* Am. Jour. Bot. **29:** 607–611. *f. 1–27.* O 1942.

Whiffen, A. J. Two new chytrid genera. Mycologia **34:** 543–557. *f. 1–52.* 1 O 1942.

White, W. L. Studies in the genus *Helotium*- II. *Lachnum pygmaeum* and the status of the genus *Helolachnum.* Am. Midl. Nat. **28:** 512–523. S 1942.

Yarwood, C. E. & Hazen, W. E. Vertical orientation of powdery mildew conidia during fall. Science **96:** 316, 317. 2 O 1942.

PALEOBOTANY

Brown, R. W. A Miocene grapevine from the valley of Virgin Creek in northwestern Nevada. Jour. Wash. Acad **32:** 287–291. *f. 1–5.* 15 O 1942.

Janssen, R. E. Fossil forests of the great Coal age. Sci. Monthly **55:** 195–208. *f. 1–19.* S 1942.

Sears, P. B. Postglacial migration of five forest genera. Am. Jour. Bot. **29:** 684–691. *f. 1–6.* O 1942.

Schopf, J. M. Contributions to Pennsylvanian paleobotany. *Mazocarpon oedipternum* sp. nov. and sigillarian relationships. Ill. Geol. Survey Rept. Invest. **75:** 1–40 *pl. 1–6.* 1941.

Schopf, J. M. Spores from the Herrin (no. 6) coal bed in Illinois. Ill. Geol. Survey Rept. Invest. 50: 1–58. *pl. 1–8.* 1938.

Wilson, L. R. & Webster, R. M. Fossil evidence of wide Post Pleistocene range of butternut and hickory in Wisconsin. Rhodora **44:** 409–414. pl. 725, 726. N 1942.

ECOLOGY AND PLANT GEOGRAPHY

Arnst, A. Vegetal stabilization of Oregon coastal dune areas. Northwest Sci. **16:** 59–67. Au 1942.

Braun, E. L. Forests of the Cumberland Mountains. Ecol. Monogr. **12:** 413–447. O 1942.

Camp, W. H. Continental displacement and the origin of the American floras. Proc. 8th Am. Sci. Cong. **3:** 193, 194. 1942.

Dugand, A. Estudios geobotánicos Colombianos: descripción de una sinecia típica en la subxerofitia del litoral caribe. Proc. 8th Am. Sci. Cong. **3:** 207–217. 1942.

Oosting, H. J. An ecological analysis of the plant communities of Piedmont, North Carolina. Am. Midl. Nat. **28:** 1–126. Jl 1942.

Potzger, J. E. Pollen spectra from four bogs on the Gillen Nature Reserve, along the Michigan-Wisconsin state line. Am. Midl. Nat. **28:** 501–511. S 1942.

Preston, R. J. The growth and development of the root systems of juvenile lodgepole pine. Ecol. Monogr. **12:** 449–468. O 1942.

Roberts, T. W. Behavior of organisms. Ecol. Monogr. **12:** 339–412. O 1942.

Shreve, F. The life forms and flora of the North American desert. Proc. 8th Am. Sci. Cong. **3:** 125–132. 1942.

Uphof, J. C. T. Ecological relations of plants with ants and termites. Bot. Rev. **8:** 563–598. N 1942.

Wells, B. W. Ecological problems of the southeastern United States Coastal Plain. Bot. Rev. **8:** 533–561. O 1942.

White, O. E. Temperature reaction, mutation, and geographical distribution in plant groups. Proc. 8th Am. Sci. Cong. **3:** 287–294. 1942.

GENERAL BOTANY
(including biography)

Balfour, F. R. S. David Douglas. Jour. Roy. Hort. Soc. **67:** 121–128, 153–162. *f. 42.* Ap, My 1942.

B[arnhart], J. H. Herbert McKenzie Denslow. Bull. Torrey Club **69:** 479. *port.* 3 O 1942.

Chamberlain, C. J. William Jesse Goad Land. Bot. Gaz. **104:** 1, 2. *port.* 12 O 1942.

Ewan, J. Botanical explorers of Colorado—II. Edwin James. Trail & Timber line 282: 79–84. Je 1942.

Fernald, M. L. Some early botanists of the American Philosophical Society. Proc. Am. Philos. Soc. **86:** 63–71. 25 S 1942.

Gustafson, F. G. Parthenocarpy: natural and artificial. Bot. Rev. **8:** 599–654. N 1942.

Johnson, E. L. Francis Ramaley. Madroño **6:** 260–265. 23 O 1942.

Kern, F. D. Joseph Charles Arthur, 1850–1942. Phytopathology **32:** 833–844. *port.* O 1942.

Pennell, F. W. Benjamin Smith Barton as naturalist. Proc. Am. Philos. Soc. **86:** 108–122. 25 S 1942.

Rousseau, J. Asa Gray et la publication de la flore de Provencher. Nat. Canad. **69:** 207–209. A-S 1942.

Silva, V. & Maciel, J. C. A. Novas teorias para a filosofia das ciências. Proc. 8th Am. Sci. Cong. **3:** 133, 134. 1942.

Wilcox, A. N. & Schmitz, H. Plant life and its economic utilization. 135 mimeographed pages. Univ. Minnesota, Minneapolis, 1942.

Yuncker, T. G. A note on the precocious germination of dodder seed. Proc. Ind. Acad. **51:** 114, 115. *1 f.* Je 1942.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 2, pp. 91 103 MARCH, 1943

EXPERIMENTS IN THE GRAFTING OF SPECIES IN THE GENUS VIOLA[1]

JOHN D. DODD[2] AND ALEXANDER GERSHOY[3]

INTRODUCTION

Cyto-taxonomical and hybridization studies of the genus *Viola* have been in progress at the Vermont Agricultural Experiment Station for a number of years. The norm of hybridization limits among the species in the various sections and sub-sections of this genus have been determined (Gershoy, 4). No intersectional crosses have been consummated although hybrids between species representing the distinct subsections of the *Nominium* section have been grown to maturity. The present investigation represents an attempt to determine what relationship exists between the capacity for hybridization and the capacity for grafting in this genus.

In order to test for a positive correlation it is necessary to demonstrate that grafting limits lie within the violet genus as represented by the species available for study. Evidence in the literature of graftage suggests that the limits are not generally confined to so small a range as a genus:

A. Mirov (8), in a recent paper, described experiments in which he found no difficulty in grafting various species of pine.

B. Intergeneric grafts in many families, particularly in the *Solanaceae*, have been an object of study by numerous workers, many of them interested in chimaeras. Jones (5) has discussed the work of Winkler, Baur, and others in this respect.

C. Daniel (3), in a review of the literature and in a discussion of his own work, had earlier shown that graft combinations are possible between unlike species of plants separated, in some cases, by greater than generic differences.

A general statement of the problem may perhaps be reduced somewhat to the following query: does a relationship exist between, on the one hand, the ability of two different protoplasms to survive in the close juxtaposition of tissues such as is afforded in a graft union and, on the other hand, the capacity of these unlike protoplasms to achieve a successful fusion of gametes?

In regard to the problem of grafting limits it should be emphasized here

---

[1] Published with the approval of the Director of the Vermont Agricultural Experiment Station.

[2] Department of Botany, Columbia University; formerly assistant in research at the Vermont Agricultural Experiment Station.

[3] Assistant botanist at the Vermont Agricultural Experiment Station.

[THE BULLETIN for January (70: 1–90) was issued December 31, 1942]

that the violet genus as recognized by Engler and Prantl (1) covers a very wide range of morphological types. It is not considered improbable, therefore, that intrageneric limits might exist. So far as the authors are aware a study of experimental graftage has not been made in the violet genus.

EXPERIMENTAL PROCEDURE

Practical considerations limited the experimental program to the determination of a fair sample of the reciprocal grafting combinations that are possible with available species. Five species were chosen for use as being representative of the wide morphological, anatomical, and physiological differences existing among the north temperature members of the genus.

DESCRIPTION OF SPECIES TYPES USED[4]

Section *Melanium:* *V. tricolor* var. *florairensis* (?) or var. *lutea* of horticultural origin (?).

This species is potentially biennial but often behaves as an annual. The axes of first and second order are erect and flowering. Flowering is continuous throughout the season. Except in the basal nodes of older stems the proportion of parenchymatous tissue is high and mechanical tissue seems to be limited to the xylem elements in the separate vascular bundles. The pith cells are ruptured by stem enlargement, resulting in hollow stems.

Section *Chamaemelanium: V. canadensis* L.

This is a perennial species. The primary axes form short, thick, fleshy rootstocks which are transversely geotropic. Secondary axes are erect and flowering. Each aerial shoot is herbaceous and exhibits rapid growth of comparatively short duration. Leaf- and flower-size diminish markedly as meristem activity dwindles. Mechanical tissue is limited to the xylem elements in the separate bundles and the proportion of parenchymatous tissue is high. Usually the pith cells are not enlarged beyond elasticity limits as judged by a lack of schizogenous areas. They are capable of some regenerative activity.

Section *Nominium,* subsection *Rostellatae: V. striata* Ait.

The basal portions of axes of first and second order become erect or inclined woody rootstocks of at least biennial duration. Flowering axes are erect or inclined. They are herbaceous and have an intact pith. There is a layer of presumably pericyclic fibers which serves to isolate the phloem tissue of each bundle from the parenchyma cells of both the cortex and the medullary rays. New leaves and flowers are developed throughout the season.

Section *Nominium,* subsection *Uncinatae: V. odorata* L.

Primary axes are quite short, erect and at least of biennial duration. In

[4] The taxonomical descriptions are adapted from Gershoy (4). Certain anatomical and histological features are added by the authors in the present paper.

such axes the amounts of cortical and pith parenchyma are relatively small. Vascular tissue becomes a complete cylinder resulting in a high proportion of mechanical conducting cells. Lateral axes form short or long, leafy runners, potentially capable of rooting at any node. The anatomy of these runners is similar to that of the primary axes although there is not as much mechanical tissue present. A terminal rosette develops into a short, erect axis resembling the primary seedling axis.

Section *Nominium*, subsection *Plagiostigma: V. papilionacea* Pursh.

Primary axes are foreshortened into thick and fleshy rhizomes which form similar, secondary axes in the axils of the leaves. Continual branching and separation of branches results in clonal clusters. Leaves are long-petioled and have broad, cordate-ovate blades. Parenchymatous tissue is inclined to be mucilaginous in older plants, particularly in the rhizome. Flowers develop in the leaf axils of the seedling rhizomes first.

The program of effecting reciprocal grafts among these five species was carried out during the summer growing seasons of 1939 and 1940. Since the north temperate species of violets grow very slowly and abnormally under warm greenhouse conditions in winter they are left in a dormant state. For this reason the study was limited to the months from May to September, i.e., between the times when the leafy branches were large enough to be used and when they became decadent in the fall.

During these two summers several hundred grafting operations were performed in an attempt to develop technics which would permit successful grafting of species with such varied morphology as those selected for study. Many of these experimental grafts were unsuccessful. However, as will be indicated elsewhere in this paper, individually successful grafts encompassed most of the planned intersectional combinations.

It was tentatively planned to attempt each interspecific combination a definite number of times and then to compare the numbers of the successes of each combination, thus putting the results on a statistical basis which might permit a conclusion as to the degree of success of any given interspecific combination.

However, it is obvious from the following considerations that such data as were obtained do not lend themselves to worthwhile statistical analysis:

1. Since a successful graft indicates that a given type combination is possible all of the unsuccessful attempts to obtain a like combination may be the result of faulty technic.

2. The successful technics were developed by the trial and error method and varied markedly from each other. It has not been possible to enlarge the experimental program in order to analyze statistically the variables involved

most closely in grafting success. Some of these variables are mentioned briefly as follows: a, time of grafting; b, relative ages of tissues in contact; c, relative areas of tissues in contact; d, pressure of bindings and protection of the graft region.

EXPERIMENTAL TECHNIC

The actual grafting technics were varied for each combination of species. The reciprocals of each interspecific combination often differed from each other, in methods used as well as tissues placed in juxtaposition. In general, however, the methods used can be classified into two well known types: sleeve grafts and whip grafts. Approach grafts were tried and abandoned since they gave poorer results than simple whip grafts and could only be used for the same types of species combinations. Bud grafts would have involved the manipulation of extremely delicate tissue and were not considered practical under the experimental conditions. Bottle grafting, as described by Blakeslee and Farnham (2), is an interesting method which, unfortunately, escaped the authors' attention until the present experiments were concluded. It will be tested later.

Seedling grafts presented a definite obstacle to many of the desired grafts since such grafts would have required a union between the swollen and fleshy primary axes of such species as *V. papilionacea* and the slender, relatively unstrengthened axes of such species as *V. tricolor*. It is impossible, in such cases, to adequately match the areas of wound surfaces. However, the seedlings of *V. papilionacea* were easily grafted to mature stems of *V. tricolor*. The hollow stems of the latter species were split open lengthwise and laid flat against the cut surface of the fleshy rhizome of the former, thus completely matching the cut surface.

In order to maintain a degree of uniformity in methods it was decided to reserve the method of seedling grafts as a separate problem and to use it in the present investigation only as a last resort when experiments with mature plants failed to yield a desired interspecific graft.

Cuts for the graftage were made with a sharp, clean razor. The stock and scion were tied together with strips of moistened cellophane tape which was found to be easier to manipulate than raffia. Each graft was bound with a narrow strip of Parafilm which was wrapped around the graft region in much the same manner as a tape bandage. The warmth of the fingers sufficed to form an adequate seal. This bandage was removed after about three weeks. A shade frame was used during the first week but it was found that continued close shading induced conditions favorable to mildew, particularly in grafts which involved *V. tricolor*, a species intolerant of shade.

INTERPRETATION OF RESULTS

At the beginning of this project it became obvious that the interpretation

of results would present a major problem. Fruit trees and ornamentals are grafted with a definite end in view which, if attained, indicates success in grafting. The present problem, however, did not lend itself to a single and immediately obvious criterion of grafting success and the selection of arbitrary tests which would define a fully successful graft became a central point in the interpretation of the results obtained.

After careful consideration it was decided that a perfect graft could be defined as one which either possessed the following characteristics or gave indications that these characteristics would be obtained were the graft carried into another growing season:

1. The graft must form a tissue union in which living cells of each member would be in immediate contact, that is, there should be no layer of necrotic tissue left between the stock and scion. Vascular continuity should be established between the stock and scion in such a tissue union.

2. The root system of the stock and the shoot system of the scion should both continue vigorous growth. The scion should develop vegetative parts of normal appearance from primordia which are laid down at some time after the grafting operation. It is necessary to make a careful distinction between continued growth of new primordia and the enlargement of parts in existence previous to grafting.

From a theoretical point of view it should be proven that the stock has utilized food material passed across the contact region by normal conduction mechanisms. The use of seedling stocks would provide a direct demonstration of this since there would be comparatively little reserve food in the primary axis and there would be no secondary axes of stock origin which would serve to feed the root system. Unfortunately, the previously explained limitations to the use of seedling stocks have prevented such a direct physiological criterion.

Some indirect evidence has arisen that stock tissue has utilized scion foodstuffs. An example of this is the graft of *V. odorata* on *V. tricolor* stock. In this graft only one of the vascular bundles in the stock formed vascular continuity with the scion. It enlarged, through cambial action, to such an extent that it became comparable, in size, to the stele of an entire normal stem. Since all connection with the original stock shoot system had been severed it seems a plausible explanation that scion foodstuffs were utilized in this hyperplastic growth of the stock.

3. Daniel's (3) postulate that, in a successful graft, the scion should mature fruit, seems to be a sound one. In order for fruiting to take place a graft union must form and the scion must continue growth. It should be emphasized again, here, that buds of the scion in existence at the time of grafting may develop to some extent without the formation of a true union. In no such case, however, have the buds shown the beginnings of swollen ovaries.

The first two criteria of grafting success could be presupposed from data showing that the scion had developed fruit from the primordia arising subsequent to graftage. Fruiting could, then, be used as a single criterion. However, it has not always been possible to adopt this test in the present work because many of the developing grafts were cut short by the advent of adverse growing conditions, coincident with the beginning of the winter period of dormancy for violets. Thus, these grafts did not survive long enough to develop fruit.

Attempts to overwinter some of the grafts, both on the original stock plants and as a form of cutting, met with failure. The apparent success of a few overwintered grafts was shown to be due to the formation of roots by the scion species.

From the preceding discussion it is evident that in the determination of its degree of success each attempted graft combination is to be treated separately. The attempted grafts are discussed individually under one of the following classifications:

A. Successful grafts.
B. Unsuccessful grafts.
C. Special cases.
   I. Grafts involving *V. canadensis* as the scion.
   II. Grafts involving *V. papilionacea* as the stock.

A. SUCCESSFUL GRAFTS

1. *V. papilionacea* on *V. tricolor* stock (fig. 3).

A seedling rhizome of the scion species was sliced diagonally so that the apex remained uninjured. The stock was decapitated and split open lengthwise on one side at the tip of the stump. The inner surface of the hollow stump was pressed against the cut surface of the scion and the graft was bound in the manner previously described.

A graft union formed and the scion developed several leaves to a normal size. No fruit was formed during the duration of this graft but the extreme vigor of growth of the scion warrants its being termed successful. Mature rhizomes of *V. papilionacea* were tried with no success, the failure being perhaps due to the inhibiting action of the mucilaginous substance which exuded from cut surfaces and which prevented a direct cell-to-cell contact between the stock and scion.

2. *V. papilionacea* on *V. canadensis* stock.

A seedling of the species used as the scion was prepared in the same manner as in the preceding graft. The stock was decapitated at the second node and a diagonal slice of such a length that the cut surface matched that

of the scion was made through the region of the node. The injured surfaces were placed together and the graft was bound.

A graft union formed and the scion developed several new leaves. It was considered, also, to be a potentially successful graft although the growth was not quite as luxuriant as in the preceding case.

3. *V. odorata* on *V. tricolor* stock (fig. 6).

The stock was decapitated and split open at the second node. A portion of a runner of *V. odorata* with a developing rosette at the tip was used as the scion. The runner was partially decorticated for about an inch and the cut surface was fitted into the hollow portion of the split internode. The scion formed several new leaves and maintained a normal appearance. No flower buds were developed before the end of the growing season. A complex graft union formed in which a vascular bundle of the stock went through a period of hyperplastic enlargement. This enlargement has been discussed previously as evidence that the stock was able to utilize scion foodstuffs.

4. *V. striata* on *V. canadensis* stock (fig. 1).

The stock was decapitated at the second node and a diagonal slice, two inches long, was made up through the internode below to the node where the shoot was severed. A four-inch tip of a lateral flowering shoot of the scion parent was cut off at the nearest convenient node. A diagonal slice was made from this basal node to the node above. The graft was bound in the usual manner.

The scion continued to develop new leaves of normal appearance throughout the summer and finally matured a small pod with one seed. This is a very small percentage of the normal seed number.[5]

5. *V. odorata* on *V. canadensis* stock (fig. 4).

The stock was decapitated at the second node and sliced diagonally as in no. 4. A portion of a runner of *V. odorata* with a terminal rosette was used as the scion. This runner was sliced diagonally so that its cut surface matched that of the stock.

A graft union formed and the scion continued normal growth. Two seed pods were matured during the rest of the season. There was one seed in each pod.[5]

6. *V. striata* on *V. odorata* stock (fig. 5).

A three-inch tip of the scion plant was cut off at the nearest node and sliced diagonally. The terminal rosette of a runner of *V. odorata* was cut off

[5] Manch (8) recorded the normal seed number for several species of violets. The seed numbers of all pods formed by scions in the present experiments were small percentages of the normal number for the species used as scions.

and the runner was used as the stock in a typical whip graft. A union formed and the scion continued to develop new leaves of normal size throughout the season. No fruit was matured and no flower buds were observed.

Although *V. odorata* has formed several unions as a scion this is, so far, the only successful graft in which this species has served as a stock.

7. *V. odorata* on *V. striata* stock (fig. 2).

A runner with terminal rosette was used as the scion. The stock was treated in the same manner as the stock in no. 5. The graft was a typical whip graft.

A union formed and the scion continued normal growth. Two seed pods were matured towards the end of the season, each containing one seed.

8. *V. tricolor* on *V. canadensis* stock.

The stock was decapitated at the second node and its cortex was removed over a length of two inches and about two thirds of the circumference. A four-inch tip of a flowering shoot of *V. tricolor* was split lengthwise at its base and fitted as a sleeve around the stump of the stock.

A graft union formed and slight vegetative growth occurred. Flower buds in evidence before the graft developed into flowers but did not develop fruit. However, *V. tricolor* does not self-pollinate readily by mechanical means although it is not self-sterile. This graft was regarded as being only moderately successful.

B. UNSUCCESSFUL GRAFTS

The grafts listed below were attempted several times, with varied technics, without success. However, the number of attempts was not statistically large enough to warrant the generalization that grafting is not possible in these cases. Special technics for these combinations have not been devised as yet.

1. *V. tricolor* on *V. odorata* stock.

The reciprocal of this, however, was successful.

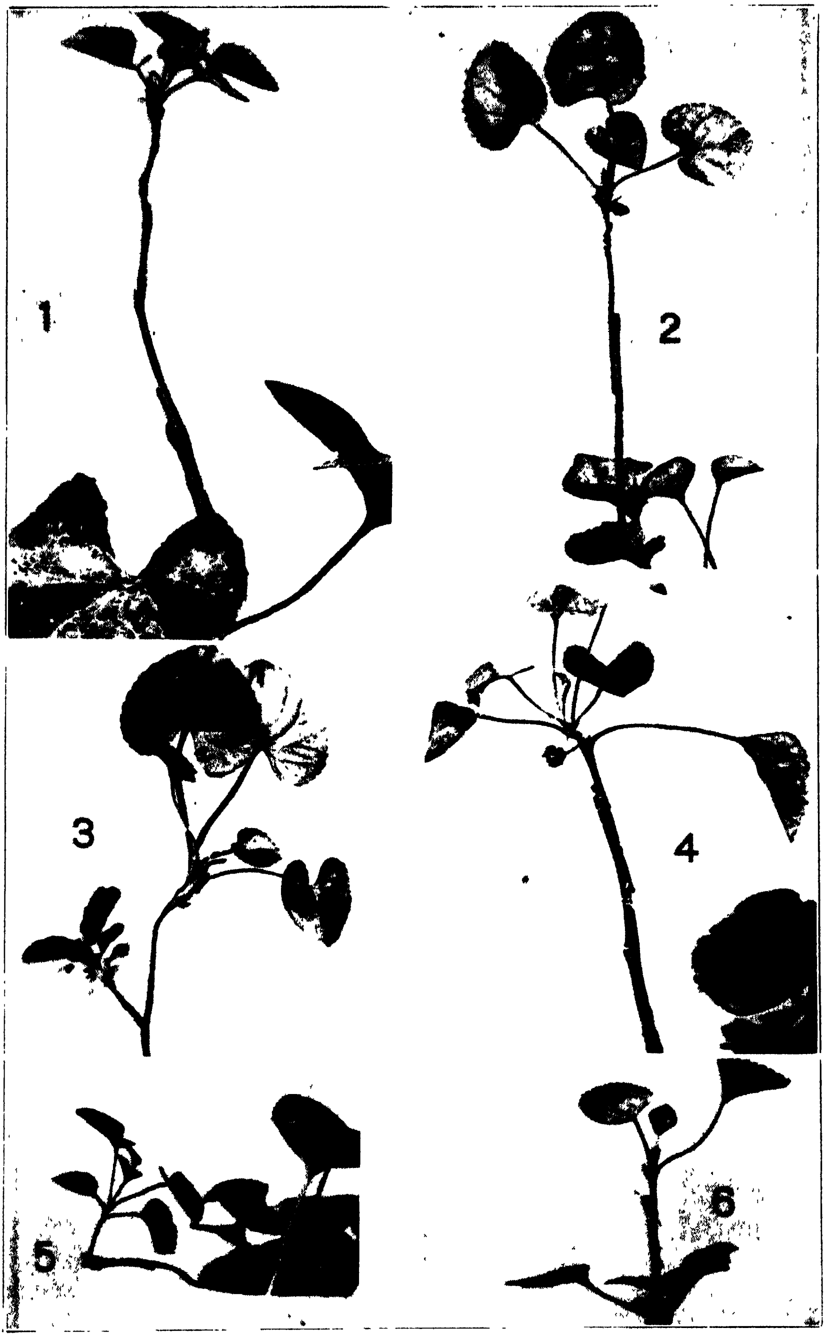
2. *V. papilionacea* on *V. striata* stock.

The reciprocals of grafts (2) and (3) are discussed under Special Cases, part 2.

3. *V. papilionacea* on *V. odorata* stock.
4. *V. tricolor* on *V. striata* stock.
5. *V. striata* on *V. tricolor* stock.

Explanation of figures 1–6

FIG. 1. *V. striata* on *V. canadensis* stock. FIG. 2. *V. striata* on *V. odorata* stock. FIG. 3. *V. papilionacea* on *V. tricolor* stock. FIG. 4. *V. odorata* on *V. striata* stock. FIG. 5. *V. odorata* on *V. canadensis* stock. FIG. 6. *V. odorata* on *V. tricolor* stock.


1
2
3
4
5
6

C. SPECIAL CASES

Several of the grafts attempted could be classed neither as successes nor, definitely, as failures. Certain morphological characteristics of one of the species involved made it difficult to devise technics of grafting which would give satisfactory results from the point of view of the arbitrary criteria previously discussed. These questionable results are here grouped together.

1. Grafts involving *V. canadensis* as the scion.

It has not as yet been possible to induce *V. canadensis* to continue growth as a scion, either as a self graft or with other species as the stocks. Mature branches form homoplastic graft unions readily and do not deteriorate prematurely. But even in such self grafts they do not continue to develop new parts. As has been pointed out previously the aerial branches of this species have a rapid growth-phase of short duration. The growth of these branches as scions in a graft as well as in the undisturbed shoot is highly determinate in the sense that meristem activity dwindles, which causes the size of leaves and flowers to fall off rapidly near the end of growth. Attempts have been made repeatedly to graft the shoots of *V. canadensis* in the growing period. However, they are so tender that they wither quickly in spite of shade protection. It is considered possible that the technic of bottle grafting may contribute pertinent data to this problem since it might permit the use of immature branches by giving them an accessory supply of water until they establish vascular continuity with the stock.

From the above discussion it is evident that only one and, on the whole, an unsatisfactory criterion of success could be used here, namely that of graft union formation by mature branches when used as scions.

The three grafts listed below existed for a period of more than two months during which time no noticeable changes in the scion, other than a slight chlorosis, were recorded.

V. canadensis on *V. tricolor* stock, a sleeve graft.

V. canadensis on *V. striata* stock, a whip graft.

V. canadensis on *V. odorata* stock, a whip graft.

The remaining graft combination, involving *V. canadensis* as the scion, in which attempts were made to graft it on *V. papilionacea* stocks is discussed below under Special Cases, part 2.

2. Grafts involving *V. papilionacea* as the stock.

As explained above this species does not produce erect, aerial shoots or runners of long-continued growth which could be used easily as stocks. Attempts to use mature rhizomes were uniformly unsuccessful. The presence of large amounts of mucilage secreted by injured rhizomes has been suggested as inhibiting a direct cell-to-cell contact between stock and scion.

The leaf petioles of this species are long and sturdy enough to warrant their attempted use as stocks. The amount of mucilage secreted by injured petioles is comparatively small and in several instances graft unions formed when petioles were used as stocks. A few parenchymatous cells were observed to have been transformed into xylem elements but vascular continuity was not established between stock and scion. Moreover, the scions merely existed without change, none of them showing any indications of continued growth. These grafts are interesting, however, from the point of view of the proliferation of cells which occurred. Such a proliferation perhaps indicates that successful grafts are possible when *V. papilionacea* is used as a stock, providing an adequate technic can be devised.

The following species were used as scions in grafts upon leaf petioles of *V. papilionacea*. The general description immediately above applies equally well to all of the resulting grafts: *V. canadensis*, *V. tricolor*, *V. striata*, *V. odorata*.

TABLE 1. *Results of Grafting Experiments in the Genus Viola*

Stocks Scions	*V. striata*	*V. odorata*	*V. papilionacea*	*V. canadensis*	*V. tricolor*
V. striata		+	O	S	O
V. odorata	+		O	S	O
V. papilionacea	S	S		S	S
V. canadensis	+	+	+		+
V. tricolor	O	+	+	S	

+ Indicates a successful graft.
O Indicates a failure not due to observed technical difficulties.
S Indicates a failure which may be due to technical difficulties and is discussed in the text under Special Cases.
Self grafts have not been included in the present study.

CONCLUSIONS

The results briefly summarized in table 1 indicate that seven out of the ten graft combinations possible among the selected representative species in each of the distinct sections and sub-sections of the genus *Viola* have been successfully consummated in at least one of the reciprocal stock and scion relationships. It may be inferred from these results that the failure of one reciprocal can find no assumed basis in phylogenetic divergences if the other reciprocal has been obtained.

It is postulated further that the failures listed above are due to technic rather than to so-called grafting incompatibilities arising in some way from

phylogenetic divergence. A discussion of possible reasons for this technical failure has been presented in the text.

The conclusions presented are (a) that grafting limits are not coincident with any morphological divisions of the genus such as those presented by Engler and Prantl (1); and (b) that there are probably no general grafting limits within the genus *Viola*. It would, of course, be an impracticable task to demonstrate the presence or absence of specific grafting incompatibilities which might exist between any of the large number of species in the genus, regardless of their relationships. The one example in the present work which is suggestive of such a condition is the failure of *V. striata* and *V. tricolor* to form a graft union in either reciprocal combination. This example, however, should be investigated to a fuller extent before any conclusions as to the failure are reached.

No serviceable correlation can be made, therefore, between grafting limits and the hybridization index as determined by Gershoy (4). In the latter work it has been shown that hybridization limits closely follow the broad morphological delineations: no crosses having been consummated between species in the major sections of the genus.

However, the section *Nominium* is divided into three distinct subsections and a few hybrids between species in different subsections are in existence. Of these, the hybrid *V. conspersa* × *papilionacea* has been discussed by Marvin (7) and by Pierce (9). *V. papilionacea* in the *Plagiostigma* subsection was used in the present work while *V. conspersa* in the *Rostellatae* subsection is closely related to *V. striata*, which formed a partially successful graft with *V. papilionacea*.

The hybrid *V. Riviniana* × *odorata*, has not yet been discussed in print. It is a vigorously growing form which is being studied in detail since it serves as a "bridging mechanism" between the subsection *Rostellatae* in which *V. Riviniana* is placed and the subsection *Uncinatae* containing *V. odorata*.[6] *V. Riviniana* is closely related to *V. striata*, which has formed successful grafts with *V. odorata*.

These data show, as might be expected, that success in grafting may parallel success in the hybridization of species to a certain extent. However, the statement that grafting limits are not correlated with the hybridization index may be made quite definite by pointing out that successful grafts have

[6] By the use of the colchicine technic the sterile F-1 hybrids have been induced to set seed. There are now in existenc, F-2, F-3, and F-4 plants which are strikingly similar in appearance. The fertile amphidiploid plants differ, characteristically, from the sterile F-1 hybrid in possessing *fewer* and somewhat shorter internodes, thicker shoots, larger and somewhat thicker leaves and flowers and, also, bigger pollen grains of which a large percentage is quite imperfect. The F-2 plants have been used in pollination with races of both parent species, thereby producing seeds of assumed back-cross origin (unpublished data). It is stated by Engler and Prantl (1) that a hybrid of this nature does not occur in the wild and, moreover, is unexpected because of the dissimilarity of the species involved.

also been obtained between species in those groups which are isolated from each other by definite hybridization barriers, i.e., the grafts *V. striata* on *V. canadensis* stock and *V. odorata* on *V. canadensis* stock have linked the *Nominium* section with the *Chamaemelanium;* the grafts *V. odorata* on *V. tricolor* stock and *V. papilionacea* on *V. tricolor* stock have linked the *Nominium* section with the *Melanium;* and the graft *V. tricolor* on *V. canadensis* stock has linked the *Melanium* section with the *Chamaemelanium.* No hybrids between species in these three sections are known to exist.

SUMMARY

An attempt has been made to determine whether or not a correlation exists between the capacity for grafting of species and the hybridization index in the genus *Viola.* Within the genus the barrier to a successful species graft centers upon a lack of adequate technic rather than upon so-called grafting incompatibilities arising in some way from the phylogenetic divergence of the species involved. This conclusion is drawn from results demonstrating potentially successful grafts in seven of the ten possible interspecific combinations among the five species chosen to represent the wide range of morphological types in the genus. There appears to be no serviceable correlation between success in hybridization of species and species grafting.

Sincere appreciation is due for the generous co-operation given by Prof. E. Matzke of Columbia University, who has made a constructive criticism of the manuscript.

Literature Cited

1. **Becker, W.** 1925. *Viola. In* Engler, A. & Prantl, K. Die natürliche Pflanzenfamilien, **21:** 363–376.
2. **Blakeslee, A. F. & Farnham, M. E.** 1923. Bottle grafting. Jour. Hered. **14:** 171–173.
3. **Daniel, L.** 1927. Études sur la greffe. Rennes.
4. **Gershoy, A.** 1934. Studies in North American violets. III. Chromosome numbers and species characters. Vt. Agr. Exp. Sta. Bull. 367: 1–91.
5. **Jones, W. N.** 1934. Plant chimaeras and graft hybrids. London.
6. **Manch, D.** 1937. Meiosis in an F-1 *Viola* hybrid and its reciprocal. Am. Jour. Bot. **34:** 678–683.
7. **Marvin, J. W.** 1936. Cell size and organ size in two violet species and their hybrid. Bull. Torrey Club **63:** 17–32.
8. **Mirov, N. T.** 1940. Tested methods of grafting pines. Jour. Forestry **38:** 768–777.
9. **Pierce, W. P.** 1936. The relation between cell, nuclear and chromosome dimensions in a sterile violet species hybrid. Bull. Torrey Club **63:** 115–138.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 104–119 MARCH, 1943

GROWTH OF FRUITS IN CATTLEYA AND ALLIED GENERA IN THE ORCHIDACEAE

ROBERT E. DUNCAN AND JOHN T. CURTIS

The *Cattleyeae*, a tribe of the *Orchidaceae* inhabiting the tropics and subtropics of the New World, contains the majority of the important commercial orchids. Its several genera, more than one thousand species, and some six thousand recorded hybrids form the basis of a one-hundred-million-dollar industry in this country alone. Four of the genera, *Brassavola*, *Laelia*, *Cattleya*, and *Sophronitis*, and their intergeneric hybrids indicated by combination names, such as *Brassolaeliocattleya*, contain the "Catts" of commerce.

The development of fruits in the *Cattleyeae* has been studied only by Veitch (1888) who gave the periods of time elapsing between pollination and fertilization, and between the latter and fruit maturation of *Cattleya labiata* var. *mossiae* and illustrated the fruit wall changes. In general his treatment is much like Hildebrand's (1863) and Guignard's (1886) with respect to other orchids. The value of these investigations, in addition to the periodicities listed, lies in the formation of the twofold concept that pollination functions in setting fruit and is necessary prior to fertilization.

Kirchner (1922) investigated the course of events after self pollination in orchids. He found three types of behavior, which led to sterility, based on inability of the pollen to germinate on the stigma, inability of the pollen tubes to grow down into the ovary, and production of seeds without embryos.

Duncan and Curtis (1942a) found phases of growth in both length and diameter of the fruits of *Phalaenopsis*, the phases being correlated with certain internal changes. These changes are fundamental physiological happenings, such as pollination and fertilization. They showed the inter-relationships of incompatibility-sterility factors to growth of the fruit. In *Phalaenopsis* there are three phases of growth in diameter, during which proliferation of the placentae culminating in the initiation of ovule rudiments, maturation of the macrogametophytes, and embryo growth respectively take place. The first phase of growth in length lasts through the first two phases of growth in diameter; the second, when present, takes place at the time of embryo growth. The maximum rate of macrosporogenesis occurs during a relatively quiescent period, as far as growth in diameter is concerned, between the first and second phases. Fertilization takes place when both growth in length and diameter is near a minimum.

Duncan and Curtis (1942b) found two phases of growth in diameter of fruits of *Cypripedium* and *Paphiopedilum*. These phases coincide with

macrogametophyte maturation and seed development, ovule rudiments being present at the time of pollination. A single phase of growth in length concludes at the time of fertilization.

Riley (1942) has pointed out that the radii passing through the septum and midrib of *Iris* fruits grow at relatively different rates but reversals in the rate of growth of the radii occur so that the one originally growing faster is then slower. These changes in rates, producing breaks in the growth curve, take place when the fruit shape shows evidence of changing. Fertilization apparently bears a relationship to one of the breaks.

MATERIALS AND METHODS

The genera, species, and hybrids used in the present study may be found in the following list:

Species	Hybrids
Brassavola nodosa Lindl.	*Brassocattleya John Linford*
Cattleya amethystoglossa Lindl. & Reichb. f.	*Bc. Jupiter*
C. bicolor Lindl.	*Bc. Marie-Marie*
C. bowringiana Veitch	*Bc. Yellow Hammer*
C. granulosa Lindl.	*Brassolaeliocattleya Dorothy Fennell*
C. guttata Lindl.	*Cattleya amabalis*
C. intermedia Graham	*C. Brussels*
C. labiata Lindl.	*C. Cadwalader*
C. loddigesii Lindl.	*C. Dupreana*
C. luteola Lindl.	*C. Enid*
C. skinneri Bateman	*C. Kitty Wren*
C. trianaei Lindl. & Reichb f.	*C. Mina*
Epidendrum ciliare L.	*C. Molly*
E. cochleatum L.	*C. Prince Shimadzu*
E. tampense Lindl.	*Epidendrum Burtonial*
Laelia gouldiana Reichb f.	*Laeliocattleya No. 19*
L. purpurata Lindl.	*Lc. No. 21*
L. tenebrosa Gower	*Lc. No. 161*
L. xanthina Lindl.	*Lc. Canhamiana*
Leptotes bicolor Lindl.	*Lc. Gomersal*
Schomburgkia lyonsii Lindl.	*Lc. G. S. Ball*
	Lc. Schilleriana
	Lc. Wellsiana
	Sophrolaeliocattleya No. 519

The studies were made at the Morris Arboretum and the botany greenhouses of the University of Pennsylvania, both in Philadelphia, and at the ranges of Dr. C. K. Schubert and the botany greenhouses of the University of Wisconsin, both in Madison.

Pollinations were cross (between clones), close (within the clone), or self (within the flower). Distant crosses were intrahybrid or interhybrid, intraspecific or interspecific. Interhybrid crosses were intrageneric or intergeneric. The number of pollinia forming the entire complement of a flower was generally used (four in *Cattleya,* six in *Leptotes*, eight in *Laelia*). There

are several exceptions caused by size of the stigmatic cavity which was sometimes too small to hold all the pollen. The most study was devoted to four forms: *Cattleya trianaei, C. bowringiana, Epidendrum tampense,* and *E. cochleatum* var. *triandrum.* Approximately 175 ovaries were measured from flower to mature fruit in all the studies.

The fruits of the *Cattleyeae* like those of *Phalaenopsis* and the *Cypripedilinae* are lined with grooves whose terminations are closely associated with the distal and proximal limits of the ovary cavity. It is not unusual, however, to find fruits whose grooves extend either somewhat down the pedicel or slightly up the beak of the ovary. Since measurements made of the pedicel and beak of the ovary do not change during fruit maturation these slight variations were disregarded and the groove length has been accepted as the length of the ovary. In later studies these limits were marked with India ink so that the distance between the same points could be measured more exactly each time. The diameter at a level about one-half the way down the ovary was marked and measurements made at this point. As the ovaries of some species enlarge the edges of certain lobes fold back, leaving an ever widening sinus in which the alternate lobes are located. The width from the enlarging edge of the wing of one lobe to that of the adjoining—in other words the width of the sinus—was measured in several series from the time of its appearance until its permanent width was reached. All measurements were made to 0.1 mm. with vernier calipers at weekly intervals. Graphs were made by plotting a moving average of the weekly percentage of total growth in length and diameter respectively.

Fruits of *Cattleya trianaei, C. bowringiana, Epidendrum tampense,* and *E. cochleatum* var. *triandrum* were removed at intervals, fixed, and sectioned for study of internal changes both in the ovary wall and ovules. When the fruits were mature the percentage of fertile seeds was determined by counting statistically significant samples of well mixed, dry seeds from each fruit. All those seeds having an opaque embryo of normal size were considered to be fertile. In some instances germination tests were used to corroborate these counts. When fruits ripened prematurely they were examined in an effort to determine the cause.

The effect of the amount of pollen on the growth of fruit was tested by varying the number of pollinia applied to the stigma. One, two, four, and

Explanation of figures 1–10

Graphs portraying the growth of fruits of ten species of the *Cattleyeae.* Growth in length is shown by solid lines; growth in diameter by dotted lines. The figures at the left of each graph represent percentage of total growth in length; those at the right percentage of total growth in diameter. FIG. 1. *Brassavola nodosa.* FIG. 2. *Epidendrum ciliare.* FIG. 3. *Laelia tenebrosa.* The last phase of growth in diameter occurs after twenty weeks and is not shown on the graph. FIG. 4. *Leptotes bicolor.* FIG. 5. *Schomburgkia lyonsii.* FIG. 6. *Epidendrum cochleatum* var. *triandrum.* FIG. 7. *Cattleya amethystoglossa.* FIG. 8. *C. bowringiana.* FIG. 9. *C. granulosa.* FIG. 10. *C. loddigesii.*

FIG 1

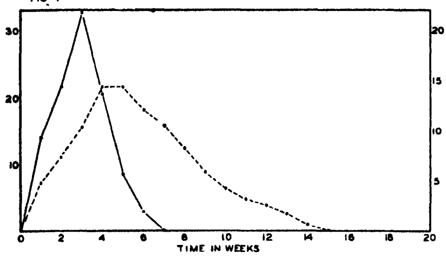


FIG 2

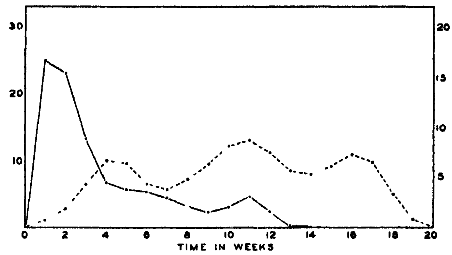


FIG 3

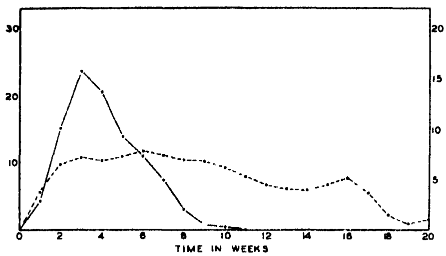


FIG 4

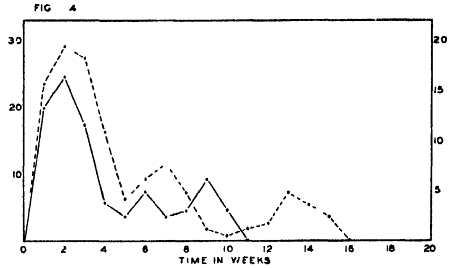


FIG 5

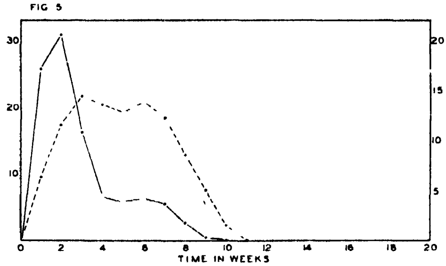


FIG 6

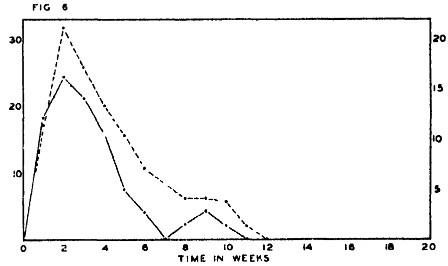


FIG 7

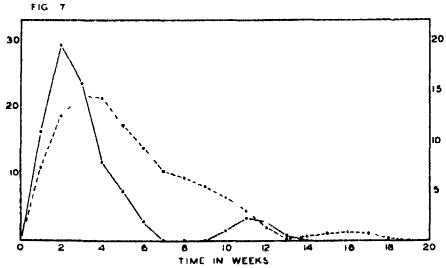


FIG 8

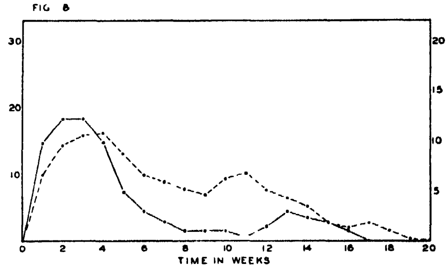


FIG 9

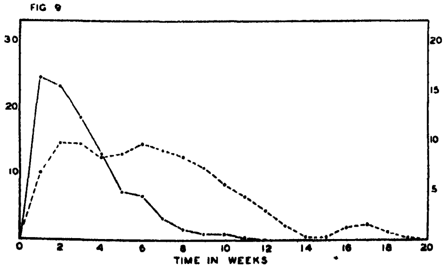
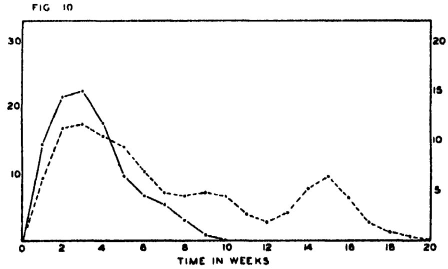


FIG 10



six pollinia were used in two series of pollinations: one series on × *Cattleya Molly;* the other, on *C. trianaei.*

Light, among environmental factors, was studied with respect to its effect on the growth of fruits. A number of flowers were pollinated on *Cattleya trianaei:* one series on plants growing in an eleven-hour day and another on plants growing in day length increased to twenty hours by two 100-watt fluorescent-tube lights.

Attempts were made to simulate the pollination effects by various chemicals and to induce fruit development by artificial means.

RESULTS

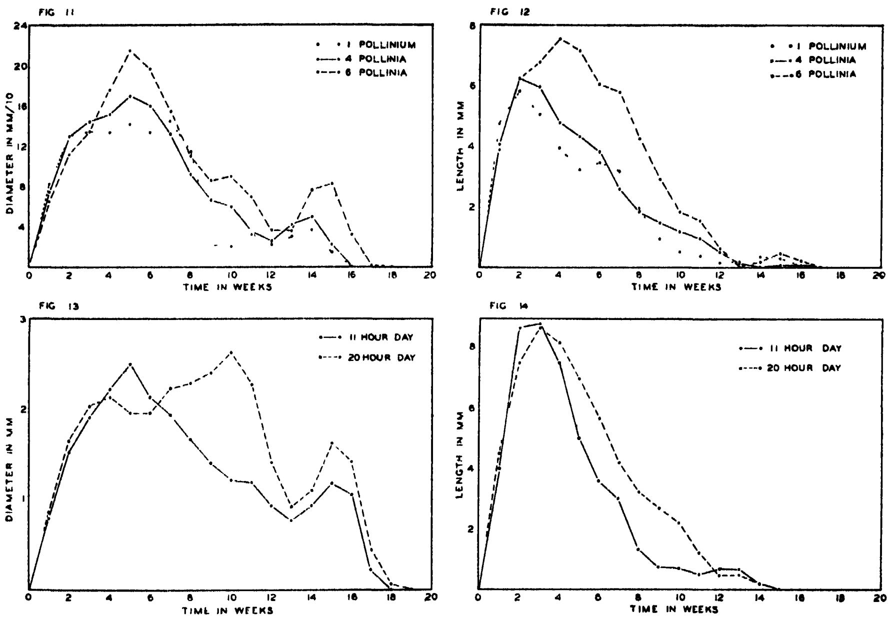
Figures 1–10 portray the growth of fruits of six genera of *Cattleyeae* and of four species within the genus *Cattleya.* All fruits represented in this group, with the exception of that illustrated by figure 5, produced seed, and are characterized by three phases of growth in diameter and one major phase of growth in length. A second and minor phase of growth in length is not always found, but when present, is associated with the third and last phase of growth in diameter.

The orchid ovary has six components which appear as lobes in cross section. Three of the components each bear a single placenta and three are sterile. Morphogenesis of the ovary wall from flower to mature fruit varies greatly from species to species of the *Cattleyeae.* For example, the six components of the ovary of *Cattleya bowringiana* are approximately of the same size in the flower and grow at about the same rate during fruit development. Flaps of the placentiferous lobes abut on each other and hide the sterile lobes until dehiscence of the fruit in certain races of *C. trianaei* (figs. 19, 23–26). The sterile lobes are hidden in the flower of *Laelia tenebrosa* but are disclosed by the widening of the sinus between the placentiferous lobes as the ovary grows. The placentiferous lobes assume a number of different forms in addition to their varying relative proportions in the fruit. Figures 15 and 17 to 20 inclusive illustrate some of these conformations. The effect of structural differences of the wall on the growth curve for diameter can be deduced by comparing the curves for *Cattleya bowringiana* (fig. 8) and *Laelia tenebrosa* (fig. 3).

The amount of pollen placed on the stigma does not alter the proportions or shape of the mature fruit but does increase the ultimate size reached in growth by the fruit (fig. 27). Figures 11 and 12 show that the weekly increments of growth in both length and diameter are increased by the application of a larger number of pollinia. Growth in length is maintained at a greater rate for a longer period of time in the first growth phase of ovaries which had been pollinated with six pollinia (fig. 12). The position and time of the interphases of growth are not affected. The peaks of the second and third phases

of growth in diameter are shifted farther apart; the duration of the interphase, in which fertilization takes place, is lengthened. The percentage (not the number) of seeds containing embryos is not significantly affected. The yields for × *Cattleya Molly* with one pollinium is 58.8 per cent; with two, 53.3; with four, 51.8; and with six, 54.2. The yields for *C. trianaei* with one pollinium is 51.2 per cent; with four, 54.0; and with six, 61.0. This series seems to indicate an upward trend with increasing numbers of pollinia but any possible significance is nullified by the results with × *C. Molly*.

Increasing the effective day length from eleven to twenty hours brings about the maintenance of growth in length and diameter at a higher rate



FIGS. 11–14. Graphs illustrating growth of fruits of *Cattleya trianaei*. FIG. 11. Increment curves of growth in diameter for three fruits of a late blooming form, each with a different number of pollinia. FIG. 12. Increment curves of growth in length for the same fruits as in figure 11. FIG. 13. Increment curves of growth in diameter for fruits of two plants of an early blooming form, each exposed to different day lengths. FIG. 14. Increment curves of growth in length for the same fruits as in figure 13.

over a longer period of time (figs. 13, 14). This is particularly true with respect to diameter; however, growth in diameter in the twenty-hour day never reaches the peak rate that is reached under the eleven-hour day. The period of slower growth between the first and second phases of growth in diameter it obscured. Neither the period of time necessary for the maturation of the fruit nor the percentage of seeds possessing embryos in a fruit is altered by the increased day length. The percentages were 55.2 for a fruit from the eleven-hour day and 52.9 from the twenty-hour day.

The following list is made up of selected crosses of various kinds. Low percentage of viable seeds is reflected to a limited extent in curves representing increments of growth in diameter.

PERCENTAGE OF SEEDS POSSESSING EMBRYOS

	Per cent
Cattleya species	
C. trianaei, cross pollinated (8)	37.6–61.4
C. trianaei, selfed (1)	0.0
C. bowringiana, cross pollinated (4)	66.7–78.3
Laelia species	
L. tenebrosa, cross pollinated (2)	48.3–64.8
Cattleya species X *Laelia* species	
C. bowringiana X *L. tenebrosa* (2)	41.7–62.1
L. tenebrosa X *C. bowringiana* (2)	6.2–19.7
Cattleya species X *Cattleya* hybrid	
C. loddigesii X × *C. Molly* (1)	63.6
Cattleya hybrid X *Cattleya* species	
× *C. Molly* X *C. labiata* (1)	64.1
Cattleya hybrid X *Cattleya* hybrid	
× *C. Molly*, cross pollinated (4)	51.8–54.2
× *C. Molly*, selfed (1)	0.0
Laeliocattleya hybrid X *Laeliocattleya* hybrid	
× *Lc. No. 21*, close pollinated (2)	17.1–17.2
× *Lc. No. 19*, cross pollinated (1)	28.0
Laeliocattleya hybrid X *Cattleya* hybrid	
× *Lc. No. 21* X × *C. Molly* (1)	11.1
× *Lc. No. 21* X × *C. Kitty Wren* (1)	36.2
Laelia species X *Cattleya* hybrid	
L. tenebrosa X × *C. Molly* (1)	87.2
Cattleya hybrid X *Laelia* species	
× *C. Molly* X *L. tenebrosa* (1)	66.6
Cattleya hybrid X *Laeliocattleya* hybrid	
× *C. Molly* X × *Lc. No. 19* (1)	64.8

The study of the internal development shows that placentae of *Epidendrum cochleatum* var. *triandrum*, at the time of pollination, has already undergone some proliferation. This is not true of *Laelia xanthina* (fig. 17) or *Cattleya amethystoglossa*. In *C. granulosa* (fig. 18) there is a certain amount of proliferation by the time the perianth expands but the placental ridges are still reflexed. *Cattleya amethystoglossa* has placental ridges which project radially toward the center of the ovary cavity; however, little proliferation has taken place by the time of anthesis. One week after pollination the ovary of *E. cochleatum* var. *triandrum* has enlarged considerably through periclinal elongation of the inner cell layers of the ovary wall. This, together with the enlargement of outer cells of the ovary wall, allows a considerable increase in the amount of ovary cavity into which the placentae have extended through enlargement of their constituent cells. Only scattered nuclear and cell divisions were seen in the ovary wall, those present being in the vicinity of the veins, the hypodermal layer of the placentiferous lobes, and the regions where dehiscence will take place at maturity. Greatly enlarged scattered cells contain either raphides or elaioplasts, both having been present in cells of the ovary of the unpollinated flower. There seems to have been a general increase in the number of cell layers in the portion of the

ovary wall adjoining the cavity but insufficient cell divisions have been seen to account for the approximately five extra cell layers of the wall. It is possible that these took place as in *Phalaenopsis* very shortly after pollination—within two or three days. The proliferations of the placentae in the week-old fruit show some scattered nuclear and cell divisions but in general the tips of the ramifications have assumed the shape of an ovule rudiment. In some cases the hypodermal cell has enlarged somewhat, and has the appearance of a primary archesporial cell.

At the end of the second week groups of pollen tubes are found growing along the sides of the placentae. The ovules show the beginnings of the first integument and a curvature. There are a considerable number of division figures in the nucellus and beginning integuments. One week later the macrospore mother-cells of most of the ovules are entering reduction division, although a few ovules contain four-nucleate macrogametophytes. At the close of the fourth week a few ovules are ready for fertilization, but the majority still contain macrospore mother cells in some stage of reduction division.

By the end of the fifth week, at the time of a second phase of growth in diameter which is very closely associated with the first (fig. 6), a greater portion of the ovules have assumed mature form and shape. During the ensuing two weeks fertilization takes place. At the conclusion of seven weeks most of the ovules contain small embryos. At the end of the ninth week, during the third phase of growth in diameter (fig. 6), the embryos have enlarged greatly, their suspensors have grown out through the micropyle and reached the surface of the placentae. The seed coats have taken on their mature texture.

The intervals at which the ovaries of other forms reach the critical points of meiosis and fertilization vary considerably. In many of the one-leaved species of *Cattleya* the first growth period intervening between pollination and reduction division in the ovules is about seventy days. Figure 28 is a photograph of the bundle of pollen tubes dissected out of a fruit of *C. trianaei* just prior to fertilization. The column and beak of the ovary which is left attached at the upper end gives an indication of the relatively large proportion of pollen tubes to ovary.

The period necessary for ripening of the fruit and the natural dissemination of the seeds varies from three months for *Epidendrum cochleatum* var. *triandrum* to fifteen for *Cattleya trianaei* under greenhouse conditions in Wisconsin.

Induction of parthenocarpy by artificial means was attempted in a series of exploratory experiments conducted over a three-year period. Fourteen species in the following genera, of which only *Laelia* and *Cattleya* belong in the *Cattleyeae*, were used as experimental material: *Cattleya, Cyrtopodium, Laelia, Miltonia, Oncidium, Paphiopedilum, Phalaenopsis, Vanda*, and *Zygo-*

petalum. Substances employed were: indole-acetic, indole-propionic, indole-butyric, and naphthalene acetic acids; Gonadogen; water and alcohol extracts of both ungerminated pollinia and pollen tubes. These agencies were tried in different concentrations in water solution, in glycerine solution, in lanolin emulsion, and as dry crystals (where possible). They were applied externally by spraying or painting, internally by injection into either the ovary cavity or the nectary, or were introduced into the stigmatic depression in cotton pellets or dry agar blocks in simulation of natural pollination.

The heteroauxins and the pollen extracts brought about wilting of the perianth in all species, except in *Zygopetalum* whose perianth segments do not wilt even after pollination. The stigma changes associated with pollination in *Phalaenopsis* were duplicated by 0.1 per cent indole-acetic acid in lanolin. The most efficient method of application was the dry agar block technique. Apparently the absorption of water by the agar influenced the water relations of the perianth in the same manner as the natural pollinia. Initial elongation of the ovary was noted in *Cattleya* (maximum elongation was 7 mm. in *C. trianaei*). In no instance did any of the treatments on any form result in fruit formation.[1]

DISCUSSION

Comparison of the growth curves of the various members of the *Cattleyeae* included in this report reveal considerable variation in length of time elapsing between pollination, meiosis, fertilization, and maturation of the fruit respectively. There is a further variation in the relative magnitude and proportions of the various parts of growth curves erected on weekly increments of growth. *Epidendrum ciliare* var. *latifolia* (fig. 2) and *E. cochleatum* var. *triandrum* (fig. 6), for example, differ greatly in the duration of the first phase of growth in diameter, the former having a considerably extended first phase. *E. cochleatum* var. *triandrum* has a second phase of growth in diameter which is greatly telescoped by the first but clearly distinct from the third. In general, however, there are three phases of growth in diameter and one, sometimes two, of growth in length of fruits of the *Cattleyeae* studied. The phases of growth in diameter coincided respectively with proliferation of the placentae and initiation of ovule rudiments, growth of the ovule and maturation of the macrogametophyte, and growth of the embryo and maturation of the seed. The first phase of growth in length is generally completed before

[1] Hubert and Maton (Parthenocarpie en groeistof. Natuurwetenschap. Tidjschr. **21**: 339–348. 1940.) have reported the production of parthenocarpic fruits of considerable size induced by the application of crystals of naphthaleneacetic acid on the stigmas of a *Cymbidium* hybrid and *Oncidium longipes*. The bearing of our own results on this report is obscure. The publication has not been available to the authors.

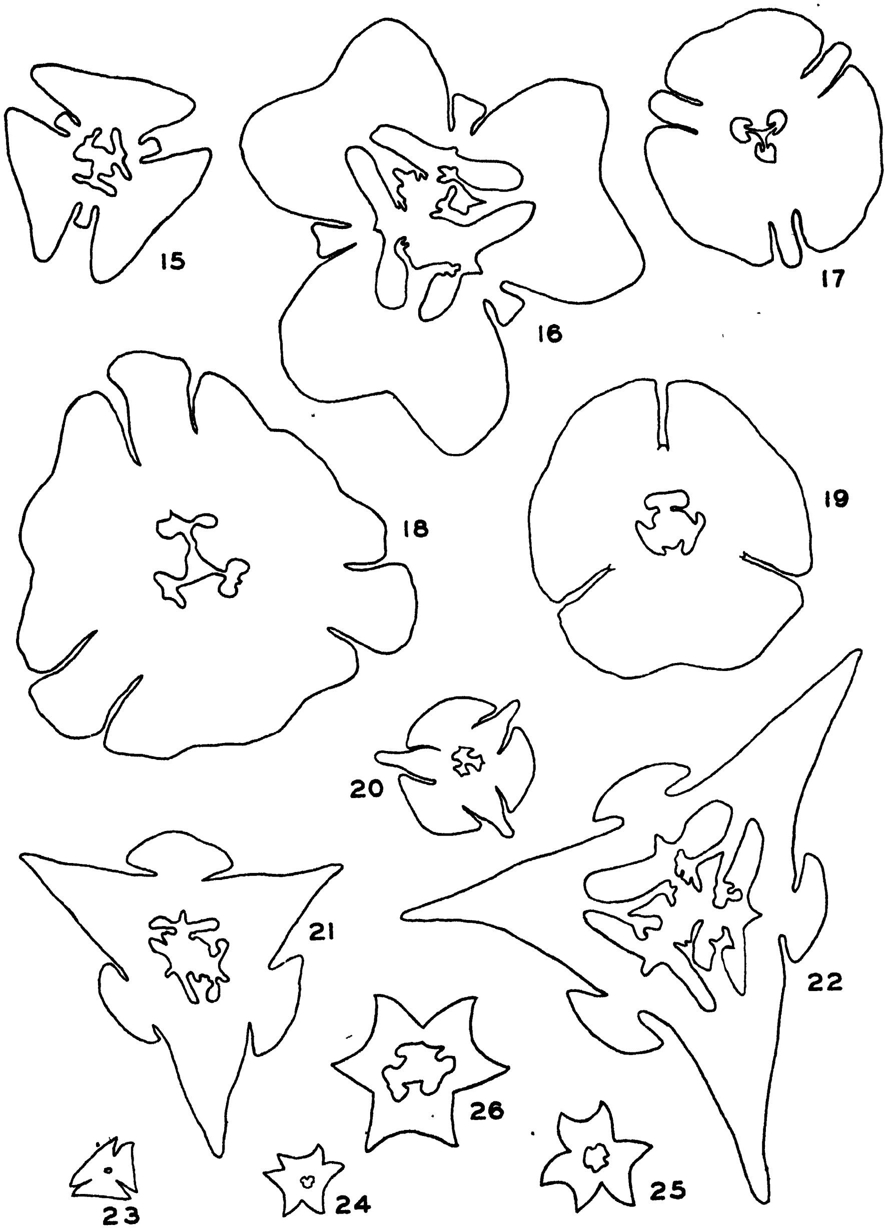
Since this paper has gone to press we have had some success in setting parthenocarpic fruit on *Zygopetalum mackayii* with naphthoxyacetic acid and naphthalene acetamide.

the end of the second phase of growth in diameter. At the conclusion of the first phase of growth in diameter meiosis is taking place. At the conclusion of the second in diameter fertilization occurs.

The first phase of growth in diameter is sometimes modified by the initiation and growth of a sinus, as in *Cattleya trianaei* (figs. 19, 23–26), between the wings of the placentiferous lobes. It is possible that telescoping of the first two phases of growth in diameter in *Epidendrum cochleatum* var. *triandrum* is caused by the growth of the singular projection of the placentiferous lobe at the time of meiosis (figs. 20–22). *Epidendrum ciliare* (fig. 2) and *E. tampense* (figs. 15 and 16), which do not possess such projections, do possess clear cut first and second phases of growth in diameter. Shortening the period devoted to each phase (climate would shorten the growing period) tends to run the phases together. *Epidendrum cochleatum* var. *triandrum* has the shortest ripening period of any member of the *Cattleyeae* studied; it is native to the northern shores of the Gulf of Mexico. The phases, of course, could be portrayed graphically more readily by the use of four-day rather than weekly intervals of measurement.

The growth of the fruit and its relation to internal changes in the *Cattleyeae* agree precisely with the development of fruits of *Phalaenopsis*. The peak rate of growth in length generally occurs at about the same time as the peak rate of growth in diameter; this feature of the *Cattleyeae* is unlike *Phalaenopsis* whose peak rate of growth in length occurs between the first two phases of growth in diameter at the time of the maximum rate of macrosporogenesis.

The chief difference between the members of the *Cattleyeae* and *Phalaenopsis* with respect to pollination effects lies in the behavior of the stigma. The edges of the stigmatic cavity of *Phalaenopsis* grow over the cavity and imprison the pollinia. This growth is brought about by enlargement of the cells making up the tissue involved. The stigma in the *Cattleyeae* remains unchanged after pollination with the exception that at times more stigmatic fluid may be secreted. Since this difference is one that mainly concerns water relations it is possible that an effect on growth could be detected. The initial lag for one or two weeks in growth in length of fruits of *Phalaenopsis* is not detected in the growth of fruits of the *Cattleyeae*. If such a lag is present it is of considerably reduced duration. A rapid initial growth in length is characteristic of the *Cattleyeae*, the only exception found being *Epidendrum ciliare*. An immediate redistribution of water under the stimulus of pollination is indicated by the simultaneous collapse of the perianth and the enlargement of tissue in other parts of the flower—i.e., the enfolding of the stigma edges in *Phalaenopsis* and the elongation of ovary wall cells in the *Cattleyeae*. The application of heteroauxins brings about these respective effects.


15
16
17
18
19
20
21
22
23
24
25
26

Growth in diameter of the ovaries of *Cypripedium* and *Paphiopedilum* is characterized by two growth phases: during the first, meiosis and development of the macrogametophyte occur; during the second, seed maturation. Fertilization takes place in the period of little or no growth between these two phases. Growth in length has concluded by this time. At the time of pollination the ovules of *Cypripedium* and *Paphiopedilum* are present and consist of a nucellus containing a distinct archesporial cell and the beginnings of the inner integument. The two growth phases in diameter in the *Cypripedilinae* are homologous to the latter two phases of growth in diameter in the fruits of the *Cattleyeae*.

Duncan and Curtis (1942b) suggested that three types of fruit development could be distinguished by the number of phases of growth in diameter, the number present being correlated with the stage of development of the ovary at the time of pollination. If the flower opens when the placentae have not undergone proliferation, three phases of growth in diameter of the ovary are present; if the flower opens when the ovule rudiments are present, two; and if the flower opens when the ovules are ready for fertilization, one. The first type should be modified, according to observations in the *Cattleyeae*, to include flowers whose ovaries contain at anthesis placentae which have proliferated to a degree but have not undergone their entire proliferation.

The differences in the development of the component parts of the fruit wall, such as the initiation and growth of wings or reflexing of the edges of the placentiferous lobes, affect the shape of the curve representing the first growth phase in diameter Since these structural changes vary from species to species of the *Cattleyeae* the curves representing growth in diameter of a species may possess a certain amount of individuality. The growth of the sinus in *Laelia tenebrosa* brings about a trimodal appearance of the first growth phase in diameter as the initiation, waxing, and waning of the growth leading to the widening of the sinus contributes to or decreases the rate of growth in diameter. Such fluctuations are emphasized by the presence of smaller amounts of pollen on the stigma as is demonstrated in *Cattleya trianaei* (fig. 11). If the six components undergo about the same develop-

Explanation of figures 15–26

Diagrams of cross-sections of orchid ovaries. FIG. 15. *Epidendrum tampense*. Cross-section of ovary of an unpollinated flower. FIG. 16. *E. tampense*. Cross-section of ovary containing seed. FIG. 17. *Laelia xanthina*. Cross-section of ovary of unpollinated flower. FIG. 18. *Cattleya granulosa*. Cross-section of ovary of unpollinated flower. FIG. 19. *C. trianaei*. Cross-section of ovary of unpollinated flower. FIG. 20. *Epidendrum cochleatum* var. *triandrum*. Cross-section of ovary of unpollinated flower. FIG. 21. *E. cochleatum* var. *triandrum*. Cross-section of ovary two weeks after pollination. FIG. 22. *E. cochleatum* var. *triandrum*. Cross-section of ovary three weeks after pollination. FIGS. 15–22. ×8. FIGS. 23–26. *Cattleya trianaei*. Cross-sections of ovaries showing the folding back of the wings of the placentiferous lobes at three, four, nine, and thirteen weeks after pollination. One-half natural size.

ment or if the proportion of sterile to placentiferous components remains about the same during the course of development, the growth curve is little affected, an example being *Cattleya bowringiana*. This is true of *Phalaenopsis*.

Since an increase in the number of pollinia applied to the stigma merely increases the size of the fruit, it may appear to be brought about by the increase in dosage of the growth regulatory compound or compounds which they contain. Extracts of the pollen, even though they do not give rise to parthenocarpic fruits, produce the same initial effects as the pollen itself. The substance responsible for fruit set may be produced by germinating pollen grains. Injections with water extracts of pollen tubes from pollen germinated on agar or on fluid of stigmas from excised columns, however,

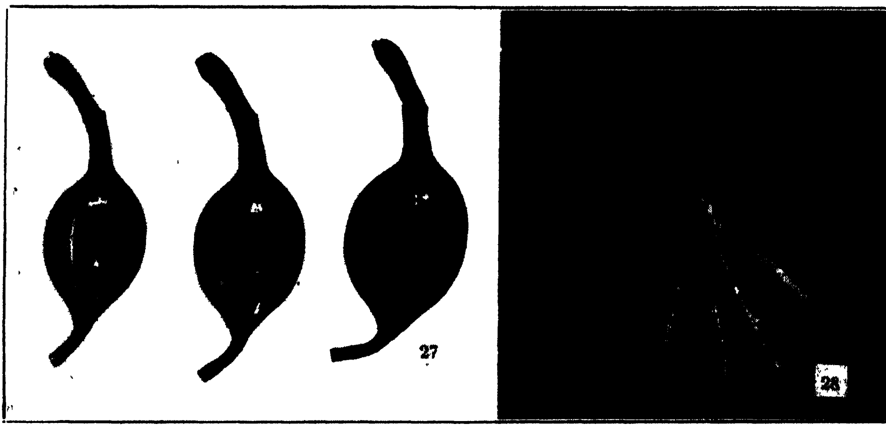


FIG. 27. Mature fruits of *Cattleya trianaei*. The smallest fruit received one pollinium, the intermediate, four pollinia, and the largest, six pollinia. The data for figures 11 and 12 were obtained from these fruits.

FIG. 28. Bundle of pollen tubes dissected from a fruit of *Cattleya trianaei* just before fertilization. The beak of the ovary is left attached to indicate the relative size of the pollen tubes.

gave negative results. This suggests that some relationship between stigmatic or stylar tissue and pollen tubes may be necessary—that one may activate the production of the growth regulatory compound in the other. These findings are in line with the conception that the entrance of pollen tubes into the ovary cavity is necessary for fruit set.

Certain of the reagents used in the work with orchids, injected into or sprayed on flowers of such plants as *Carica papaya* and *Lycopersicon esculentum*, caused ripening of parthenocarpic fruits. Although our experiments are by no means exhaustive, it would appear that the substances responsible for fruit set in the *Orchidaceae* are different from, or at least are not acti-

vated by, the same substances that Gustafson (1938) found to be effective in a wide range of dicotyledonous genera.

Figure 5 illustrates the fact that a fruit set with incompatible pollen never passes through all the growth phases of the fruit but ripens prematurely. This close mating belongs to the category of incompatibility in which germination of the pollen and entrance of the pollen tubes into the ovary take place but fertilization fails, the apparent cause being the inability of the pollen tubes to grow out to any great extent over the extremities of the placentae. The ovules do not become seed-like. Two earlier occurring types of incompatibility, the inability of the pollen to germinate on the stigma or of the pollen tubes to grown down through the stylar tissue, fail to do more than hold the ovary on the inflorescence for longer than a few weeks, abscission taking place at the base of the pedicel. The fruit of × *Cattleya Molly*, given in the list of "percentage of seeds possessing embryos" as zero per cent, contained ovules whose integuments were of mature size and texture. The curve representing growth in diameter of this fruit suggests a third growth phase. It is possible that the cause of this type of sterility lies after fertilization. The third phase of growth in diameter in corresponding fruits of *Phalaenopsis* was not detected, and this type of sterility was grouped with those in which the pollen tubes fail to grow out over the placentae and the fruit ripens prematurely. These, too, may have been brought about by post-fertilization failures. Fruits affected by this type of sterility ripen somewhat prematurely. The difficulty in assigning the cause in such chance cases lies in the fact that by the time the fruit has ripened the tips of the pollen tubes have disintegrated.

The list of percentage of seeds possessing embryos brings out several facts that should be of interest to the practical breeder of orchids. As far as general breeding work is concerned they offer nothing new. Mating members of a species with other members of the same species seldom results in exceptionally high seed set. The section of the genus *Cattleya* to which *C. bowringiana* belongs, the *Diphyllae*, yields the highest counts Reciprocals by no means give equally good results. The cross between *Laelia tenebrosa* and *Cattleya bowringiana* is an example. The cause of the inequality between the reciprocals may lie in the great difference in the length of the beak of the ovary in *Laelia tenebrosa* and *Cattleya bowringiana* and corresponding differences in the length of their pollen tubes.

× *Cattleya Molly* is an extremely heterozygous hybrid. It includes five species in its ancestry, no one of which is duplicated. When self- or close-pollinated the percentage of seeds containing embryos is low (0.0 per cent and 9.6 per cent respectively). Back crossing on the species, *C. labiata*, does not increase the yield over that of wide crosses with a member of another genus, *Laelia tenebrosa*, or with intergeneric hybrids such as × *Laeliocattleya*

No. 19 although it does increase the yield over crosses between different plants of × *Cattleya Molly*. It is interesting to note that the fertility of × *C. Molly* is about the same as that of *C. trianaei*, a species.

The complex intergeneric hybrids *Laeliocattleya No. 19* and *No. 21* show more sterility than × *Cattleya Molly* when close pollinated or when individual plants of the respective hybrids are mated among themselves. There is, however, a wide range of fertility when used as either a pollen or a female parent in a wide cross. Since there is a certain amount of back crossing on species in their ancestry the individual plants of each hybrid may behave quite differently. This may explain the wide range of values. × *Laeliocattleya No. 21* shows more sterility than × *Lc. No. 19*. The intergeneric hybrids between species of *Brassavola* and *Cattleya*, like those between *Laelia* and *Cattleya*, have considerably reduced fertility. The percentage of seeds possessing embryos was not determined for hybrids whose ancestry includes three or four genera.

It is perhaps not surprising that the orchids, which have evolved such a high degree of specialization to insure cross pollination, should give higher percentages of good seeds when matings are between clones. The cleistogamous orchids, however, according to Kirchner (1922) are highly fertile. It is surprising, however, that crosses between members of different species or even genera should give better results than selfing. This emphasizes the fact that the barriers between species and genera in the *Cattleyeae* are slight. During the past sixty years of breeding only two groups, relatively incompatible with other members of this tribe, have been found. They are the reed-like section of *Epidendrum* and the Mexican section of *Laelia*.

SUMMARY

The type of fruit development first described in *Phalaenopsis* is found in the *Cattleyeae*.

The basic trimodal growth curve may be modified by the specific conformations of the fruit wall and the relative growth rate of the components.

The amount of pollen affects the ultimate size but not the proportions of the fruit.

Increasing the day length contributes toward a larger fruit.

Neither light nor a variant amount of pollen, within reasonable limits, significantly affect the percentage of seeds possessing embryos.

Three incompatibility types and probably a type of sterility caused by a post-fertilization failure are described.

Compilation of the percentages of seed possessing embryos indicates that selfing lowers the yield and wide crosses (between genera or species) often give as good a yield as crosses within a species. Extreme hybridity points

out the lack of well defined barriers to breeding between species and genera; this is correlated with their systematic classification.

DEPARTMENT OF BOTANY, UNIVERSITY OF WISCONSIN
MADISON, WISCONSIN

Literature Cited

Duncan, R. E. & Curtis, J. T. 1942a. Intermittent growth of fruits of *Phalaenopsis*. A correlation of the growth phases of an orchid fruit with internal development. Bull. Torrey Club **69**: 167–183.

——— - ———. 1942b. Intermittent growth of fruits of *Cypripedium* and *Paphiopedilum*. A correlation of the growth of orchid fruits with their internal development. Bull. Torrey Club **69**: 353–359.

Guignard, L. 1886. Sur la pollinisation et ses effets chez les Orchidées. Ann. Sci. Nat. VII. **4**: 202–240.

Gustafson, F. G. 1938. Induced parthenocarpy. Bot. Gaz. **99**: 840–844.

Hildebrand, F. 1863. Die Fruchtbildung der Orchideen, ein Beweis fur die doppelte Wirkung des Pollens. Bot. Zeit. **21**: 329–333; 337–345.

Kirchner, O. von. 1922. Uber Selbstaubung bei den Orchideen. Flora **115**: 103–129.

Riley, H. P. 1942. Development and relative growth in ovaries of *Iris fulva* and *I. hexagona* var. *giganticaerulea*. Am. Jour. Bot. **29**: 323–331.

Veitch, H. 1888. On the fertilization of *Cattleya labiata* var. *mossiae* Lindl. Jour. Linn. Soc. **24**: 395–406.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 120–125 MARCH, 1943

A MYCORRHIZOME FROM THE CARBONIFEROUS OF ILLINOIS[1]

HENRY N. ANDREWS AND L. WAYNE LENZ

In a recent description of a petrified Coenopterid fern stem from the middle Pennsylvanian of Illinois the senior author mentioned the presence of abundant mycelium in the cortical cells and suggested that they might be of a mycorrhizal nature (Andrews 1942). A detailed study of this associated fungus leaves little doubt that that supposition was correct and the abundance of the fungus, its exceptionally fine preservation, and the diversity of the morphology presented renders a description desirable.

Fossil mycelium is not uncommon. It has been reported in Carboniferous plant remains and is frequently encountered in Cretaceous and Tertiary lignites. Unfortunately the hyphae rarely display significant diagnostic characters. The only records of fossil mycelium that may with little question be considered mycorrhizal are those described by Weiss (1904) and Osborn (1909) from the Coal Measures of England. The fungus described by Weiss was found in an unidentified root (or rhizome?) and was given the name *Mycorhizonium*. It may be well to point out that that name was used as a monomial and consequently is not valid as a generic designation. It seems highly probable, however, that Weiss' interpretation of the mycelium as mycorrhizal is correct and his contribution is of significance since it shows that such an association existed in Carboniferous times. The organism described below fully confirms this and adds appreciably to our knowledge of the morphology of the Paleozoic forms. A glance at the figures may, moreover, eliminate any doubt that botanists may harbor about the quality of preservation to be found in American coal balls.

The mycorrhiza reported by Osborn was found in the cortical cells of *Amyelon radicans*. He observed "large knob-like growths with thickened walls that are apparently terminal on the hyphae, and are about .05 mm. in diameter. These I take to be a form of resting body which the fungus forms to carry it over the period during which the cortex will be sloughed . . ." (p. 607). These structures are possibly comparable to supposed vesicles described here in our Illinois specimens.

The fungus occurs in the cortical cells of a fern stem, possibly a rhizome, described as *Scleropteris illinoiensis* (Andrews 1942). The mycelium is found within the host cells throughout the cortex although it is somewhat more abundant in the middle and inner regions. Hyphae were also found in

[1] A study aided by a grant from the Penrose Fund of the American Philosophical Society.

the tracheids of the stele although they do not assume the typical mycorrhizal form in these cells.

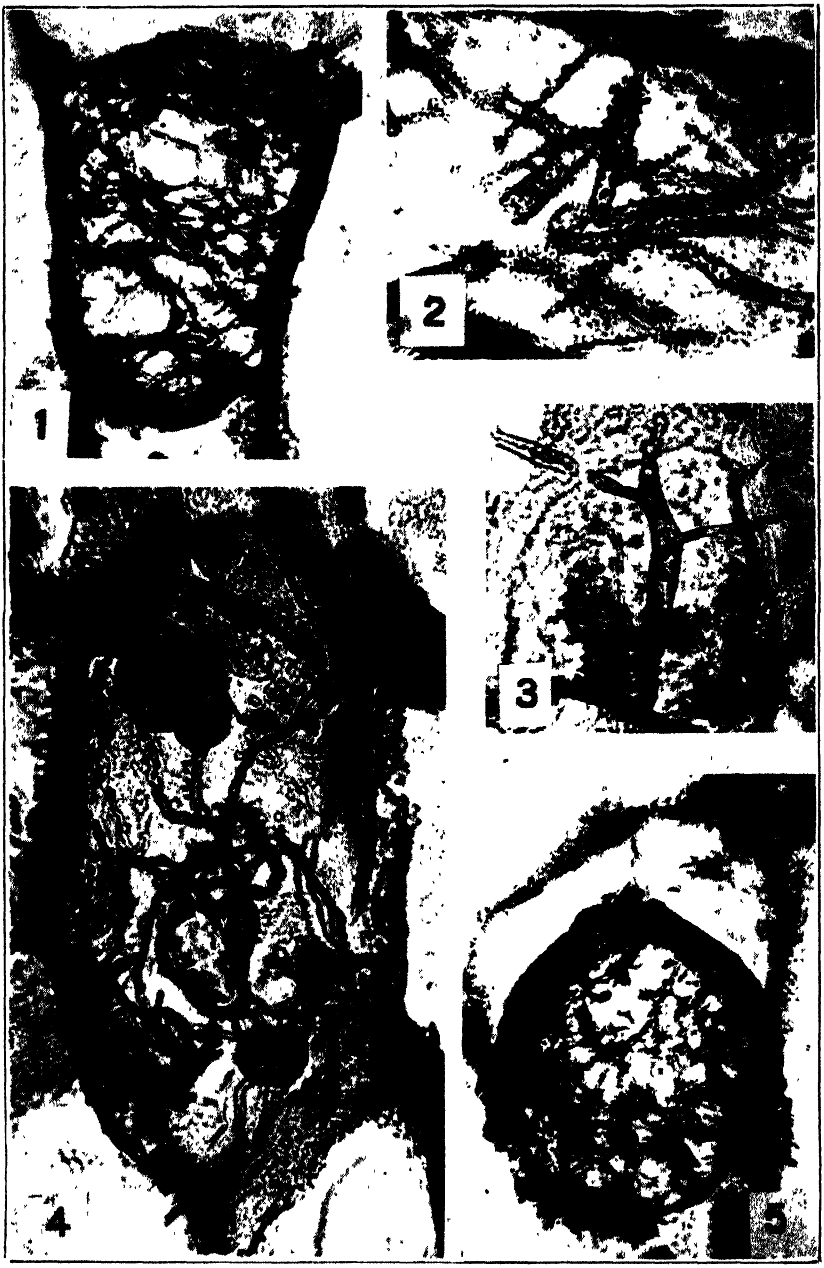
The proper application of the term mycorrhiza may be considered at this point in view of the anatomical nature of the host organ. As stated above the latter is a stem consequently the word mycorrhiza is hardly appropriate. In view of the fact that the fungus is infecting or living symbiotically with a stem or rhizome the term mycorrhizome seems more suitable and will be used in our description.

A glance at the figures reveals the diversity of the hyphal morphology. Whether or not all of this mycelium belongs to the same species of fungus cannot be stated positively. However, all of the figures are taken from the same host specimen and all within a few millimeters of each other. Although most of the mycelium seems to be intracellular, appearing typically endotrophic, there is some evidence that it may be intercellular as well. In figure 6 it appears as though some hyphae may be intercellular with branches or branching haustoria penetrating into the cell lumen. The dividing line between ectotrophic mycorrhizae or mycorrhizomata is probably not so sharp as was once supposed. Indeed Young (1940) states that "The difference between the two types of mycorrhizae is now known to be one of degree rather than of quality. They merge into one another and many intermediate forms are known."

A considerable number of host cells contain a very dense aggregation of mycelium (figs. 1, 9). It was the characteristic appearance of these cells that first attracted our attention and suggested their mycorrhizomatal nature. The hyphae average about 1 μ or less in diameter and are more or less uniformly distributed about the periphery of the cell lumen. There is some similarity between this organization and the Hartig net of the mycorrhizae of living plants. However, the slender much branched hyphae shown in these figures are clearly intracellular thus the comparison is only a superficial one. In many of the host cells infected in this way the mycellium tends to assume a nearly spherical form (fig. 5). Not only does it aggregate into compact spherical masses but as this continues the hyphae seem to become irregularly fused together, losing their identity as individual strands. This apparent fusion continues until in some cells the entire mycelial body appears as a nearly uniform amber-colored sphere.

It is perhaps most probable that this has resulted from plasmolysis of the entire contents of the host cell, but there is the possibility that this transition is the result of the digestion of the fungus by the host cells, which thus retain a symbiotic balance between host and fungus as reported in the Orchidaceae (Rayner 1927, p. 67).

Many of the cortical cells of the host harbor but a few strands of branching mycelium. These usually consist of rather large uniform hyphae bearing



FIGS. 1–5. A fossil mycorrhizome from Illinois. FIG. 1. WCB90B–S13. FIG. 2. WCB90B–S34. FIG. 3. WCB90B–S34. FIG. 4. WCB90B–S34. FIG. 5. WCB90B–S13. All figures × 500.

noticeably smaller branches (fig. 3). Filaments such as those shown in figure 8 average 6 μ in diameter while those in figure 4 are about 2 μ wide. The comparatively large size of some of the hyphae is clearly shown in figures 2 and 3, both of which are magnified 500 times, while those in figure 8 are magnified but 350 times. We have occasionally observed cross walls in these larger hyphae but they are rare and in most cases there is no evidence of septation.

Some of the other distinctive fungal features may now be considered. The type of mycelial development illustrated in figure 6 occurs in many cortical cells. It has been suggested that these knotty outpocketings of the hyphae may represent an initial stage in the development of the peripheral net of figures 1 and 9. This is probably not the case since the mycelium of infected cells such as those shown in figures 1 and 6 and always quite distinct. We have not observed any phase that might be considered intermediate between the two. Furthermore the hyphae of figure 6 are notably of greater diameter than the hyphae of figures 1, 5, and 9. It may be that figure 6 represents a specialized haustorial type of hyphae.

In a few of the cortical cells (fig. 4) there may be noted a number of larger bodies varying from 15 to 33 μ in diameter. Although we have not been able to observe the actual point of attachment it is probable that these bodies have had their origin from the swollen tip of a hyphal branch and we tentatively consider them to be comparable to the vesicles described in recent mycorrhizae. In a few of the cortical cells the larger hyphae exhibit a peculiar warty appearance (figs. 2, 7). It is difficult to be certain whether this appearance is due to minute protrusions of the hyphae or simply an aggregation of granules. Janse (1897, p. 65) has described a somewhat similar appearing accumulation of starch granules about the nuclei in *Ophioderma*. However in our material the "granules" appear to exist in organic connection with the large hyphae and we are inclined to favor the former interpretation.

In view of the wide diversity of the hyphal morphology (cf. figs. 2, 4, 6, 9) it seems likely that more than one species of fungus is represented. Furthermore our assumption that the association represented is actually mycorrhizomatal and not simply pathological is based on a general comparison with living forms. The dense tangles of mycelium shown in figures 1 and 9 compare closely with many described living mycorrhizae and if the more or less ovoid bodies shown in figure 4 are true vesicles this adds considerable weight to their supposed mycorrhizomatal nature. It has been suggested that the fungus shown in figure 6 is similar to that found in some pines.

Although the previously mentioned works of Weiss and Osborn as well as the present contribution must be considered only as introductory, the

FIGS. 6–8. A fossil mycorrhizome from Illinois. FIG. 6. WCB90B–S30. FIG. 7. WCB90B–S30. FIG. 8. WCB90B–S34. FIG. 9. WCB90B–S13. Figures 6 and 9, × 500; figures 7 and 8, × 350.

evidence accumulated to date rather strongly evinces the existence of this type of association as early as Pennsylvanian times. In view of the already proven important part that mycorrhizae or mycorrhizomata play in so many living plants it is to be hoped that the fossil record may continue to reveal significant fragments of their ancestral development.

We are especially indebted to Dr. Arthur P. Kelley and Prof. P. R. Gast for assistance in interpreting the fungi described here, although those authorities are in no wise responsible for the views that we have expressed.

BOTANY DEPARTMENT, WASHINGTON UNIVERSITY
ST. LOUIS, MISSOURI

Literature Cited

Andrews, H. N. 1942. Contributions to our knowledge of American Carboniferous Floras. I. Ann. Mo. Bot. Gard. **29**: 1–18.

Janse, J. M. 1897. Les endophytes radicaux de quelques plantes javanaises. Ann. Jard. Bot. Buit. **14**: 53–201.

Osborn, T. G. B. 1909. The lateral roots of *Amyelon radicans*, Will. and their mycorrhiza. Ann. Bot. **23**: 603–611.

Rayner, M. C. 1927. Mycorrhiza, an account of non-pathogenic infection by fungi in vascular plants and bryophytes. London.

Weiss, F. E. 1904. A mycorrhiza from the Lower Coal Measures. Ann. Bot. **18**: 255–266.

Young, H. E. 1940. Fused needle disease and its relation to the nutrition of pine. Queens. Agr. Jour. **53**: 374–392.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 126–138 MARCH, 1943

SOME FOSSIL FUNGI FROM MINNESOTA[1]

C. O. ROSENDAHL

Several years ago in the course of studying a collection of fruits, seeds, and other plant remains of Pleistocene age obtained from a deep well situated near the village of Bronson in southeastern Kittson County, Minnesota, I discovered a number of small clusters of brown sporangia-like bodies on branching thick-walled hyphae (fig. 1). The vegetable mixture in which they occurred had been recovered from clods of silt brought up in the slush-bucket in the process of drilling the well and had been freed of silt by washing through a fine-meshed wire screen. Whether these clusters had been intimately associated with plant fragments or occurred scattered through the silt matrix was not ascertained. In no case, however, were they found in organic connection with fragments of roots, leaves, bark, or other vegetable material. Superficially the organism resembled a mold, but the thick-walled, irregular hyphae and the aberrant "sporangia" clearly indicated that it did not belong in the Mucorineae. After several unsuccessful attempts to get the organism identified or to obtain a clue to its possible relationship it was reluctantly put aside as probably indeterminable. Most likely it would have remained permanently shelved except for the kindly interest of Dr. G. Bisby, of the Imperial Mycological Institute of Kew, who had seen a preparation of the material. He called my attention to a paper by Dr. E. J. Butler (1939) entitled "On the occurrence and systematic position of the vesicular-arbuscular type of mycorrhizal fungi," which had been published a few weeks earlier in the Transactions of the British Mycological Society.

In addition to his treatment of recent forms of the fungus (*Rhizophagus*) Dr. Butler also described and figured a representative of the group obtained from glacial clays underlying muskegs in the neighborhood of Edmonton, Alberta. A comparison of the Bronson well organism with Dr. Butler's illustrations, further supported by the descriptive details, soon convinced me that it belonged to the same group as the one from the Alberta bogs.[2]

The Bronson well fungus was found at a depth of 88–89 feet. The vegetable layer in which it occurred appears to have been a forest floor, perhaps of a spruce-tamarack bog, judging from the abundant remains of these trees, together with northern bog mosses. That the site had passed through the successional stages from open water to bog is evidenced by the occurrence

[1] This investigation has been aided in part by a grant from the Graduate School of the University of Minnesota.

[2] In subsequent correspondence with Dr. Butler he has confirmed this view after seeing a photograph of the Minnesota material.

of numerous fruits of several species of *Potamogeton, Najas flexilis, Zanichellia palustris, Sparganium eurycarpum* and of several species of mat-forming sedges. Over the vegetable layer rested the boulder clay of the ground moraine of the last Wisconsin ice sheet, topped by 17 feet of glacial Lake Agassiz silt. The plant deposit therefore dates back to at least the last interglacial interval.

A year or so after the discovery of the fungus at the Bronson well site it was again found in association with a plant-bearing stratum situated 36 feet deep in Lake Agassiz silt at Moorhead, Minnesota. The vegetable layer, reported to be nearly two feet thick, was encountered in the course of excavating for a sewage disposal plant located on the banks of the Red River. The present banks of the river are considerably below the flat surface of the original Lake Agassiz bottom, yet according to Professor C. A. Ballard, of the Moorhead State Teachers' College, the silt deposit overlying the vegetable stratum showed between 1800–2000 distinct varves. Leverett and Sardeson (1932) estimate that the River Warren, the outlet of Lake Agassiz, subsided some 8000 to 9000 years ago. On the basis of this estimate it is fairly safe to assume that the vegetable layer at Moorhead, buried 36 feet deep in the lake silt, was laid down at least 11,000 years ago.

As with the Bronson well material, it was not established whether the fungus occurred only intimately associated with vegetable debris or if it was also distributed throughout the contiguous silt The latter possibility is suggested by the fact that it was also recovered from lumps of the surrounding silt which were practically devoid of larger plant fragments. In any event, it was present in greater abundance than at the former site, but it occurred in identically the same form, i.e., in small isolated clusters of vesicles and hyphae (fig. 2).

During the past year the same organism (fig. 3) was recovered from a layer of plant remains encountered at a depth of 110 feet in a well near the village of Jackson in southwestern Minnesota. Fruits and seeds of more than a dozen species of angiosperms have been identified from this deposit, several of which are identical with those from the Bronson and Moorhead sites. The well is located on the Altamont moraine of the late Wisconsin drift and glacial deposit is of considerable depth at this place. The plant-bearing stratum can therefore hardly be of later origin than the last interglacial interval.

The fungus illustrated in Dr. Butler's text-figure 2, A–D, came from the basal one inch of amorphous peat resting upon the blue clay. Professor Lewis, who submitted the specimens from the Alberta bogs to Dr. Butler, stated that fungus material of the same character occurs in the pure clay, sometimes associated with fragments of leaves and branches of *Sphagnum*. In material of more recent peat from the same region Dr. Butler found a


2
1
4
3
5
6
7

closely similar fungus, but which differed from the former in having smaller vesicles that showed no tendency to form second vesicles by proliferation into the cavity of the first. The mycelium and vesicles of this form are stated to resemble in all respects the common endophyte of modern plants and in one instance the organism was found in mycorrhizal association with a root obtained at a depth of 3 dm. from the surface. It occurred throughout the peat down to a depth of 1.23 m.

The conclusions Dr. Butler reached regarding the relation of the organisms occurring in the two strata is best stated in his own words, which are as follows: "That the fungi in the glacial clay and in the overlying more recent peat are closely allied, there can be no question; except for the single fact that the older vesicles show proliferation they might be regarded as the same species."

The specimens obtained from the three Pleistocene sites in Minnesota are morphologically indistinguishable (figs. 1, 2, 3). The hyphae are somewhat tortuous, thick-walled and pale yellow in color. They vary in size but are mostly 9–11 μ in diameter. They are nonseptate, except for the rare occurrence of a cross wall in the stalk of the vesicle. The branching is subdichotomous, at an obtuse angle (figs. 2, 3), and there are occasional short diverticula and frequent unilateral projections at irregular intervals. The vesicles vary in shape from ovate to short pear-shaped and subspherical. They range in size from 75 to 103 μ in diameter and from 79 to 124 μ in length. The average of a fairly large number of measurements is 89 × 97 μ. Under medium magnification of a binocular dissecting microscope they appear dull brown in surface view, but in the sharp focus of a compound microscope the thick wall has a distinctly lemon-yellow color. Many of the vesicles were observed in open communication with the hyphae, but a few, apparently fully mature, were found occluded by a basal plug as shown in Dr. Butler's text-figure 2-A, and in some by a septum a short distance down in the stalk. The formation of a second vesicle within the first by proliferation of the stalk, in the manner described by Dr. Butler, was not seen in any of the material, although two vesicles showed a closely similar behavior. In

Explanation of figures 1–7

FIGS 1–3. *Rhizophagites butleri.* FIG. 1. Cluster of vesicles and hyphae from the Bronson well deposit, depth of 88–89 feet. × 50. FIG. 2. Smaller cluster from a layer of plant remains in Lake Agassiz silt at Moorhead, Minesota, depth of 36 feet. A portion of a decaying root is shown at the right. × 91. FIG. 3. Specimen from a well near Jackson, Minnesota, depth of 110 feet. The wall of the single vesicle is somewhat collapsed. × 91.

FIGS. 4–7. *Rhizophagites minnesotensis*, showing several clusters of hyphae and vesicles, all obtained from an early Pleistocene deposit at Springfield, Minnesota. FIG. 4. Fungus in association with a root. × 91. FIG. 5. shows two vesicles intact but much blackened. × 91. FIG. 6. shows a cluster of tangled hyphae and many vesicles, some of which are partly collapsed. × 50. FIG. 7. shows two vesicles from upper left-hand corner of figure 6, more highly magnified, also shows more clearly the variation in thickness of the hyphae and their manner of branching. × 91.

most of the older vesicles the contents become surrounded by a second wall which merges with the original wall at the neck of the stalk as shown in figures 13 and 14, or it may even extend funnel-like a short distance down into the stalk. In the latter case a thin septum may or may not be present in the stalk. This second wall ultimately becomes nearly as thick as the outer one, and the thickening obviously begins at the distal end of the vesicle and progresses towards the base (fig. 2). In a few vesicles the contents appeared as a spherical mass surrounded by an evenly thick second wall without any visible connection or contact with the outer wall (fig. 3). These differences in the internal appearance of the vesicles probably denote only different stages of their development, yet the presence of basal plugs, and of septa in some vesicles and not in others, shows that structural variations occur. The proliferation of the stalk observed by Dr. Butler is probably a more pronounced manifestation of the phenomenon.

Even though it has not been possible to duplicate in any of the Minnesota material this proliferating process, the organism otherwise agrees so completely with that from the Alberta bogs that it is fairly certain the same species of fungus is involved. The fact that it occurred widely in similar habitats, i.e., in glacial clays associated with remains of other plants, and has not hitherto been observed in material of more recent origin, indicates that it represents a species that flourished under the conditions of the Pleistocene and which probably became extinct at the end of that period.

While there is as yet no record of the certain occurrence of the species earlier than the last interglacial interval, evidence has recently come to light of the existence of the group at the beginning of the Pleistocene. This rests on the discovery two years ago of a very closely similar organism (figs. 4–7) in a piece of silt-imbedded peat that came from the line of contact between Cretaceous shale and Nebraskan till near the bottom of a preglacial gully on the property of the Ochs Brick Company at Springfield, in Brown County, Minnesota.

The hyphae of the fungus from this site are somewhat more irregular in form than the one discussed above (fig. 17), but they show the same characteristic branching, irregular projections, and color as the other. The vesicles are darker in color, less numerous, and considerably smaller (figs. 4–6), ranging from $42 \times 46\ \mu$ to $58 \times 61\ \mu$. They show the same type of second wall formation within as described above (figs. 15, 16). Both hyphae and vesicles look somewhat battered as compared with those from the younger sites, but it is surprising that any structure so fragile could have endured so long in the compacted peat without complete collapse or disintegration. The peat in which the organism was found was made up largely of mosses of which the most abundant were *Camptothecium woldenii, Campylium stellatum, Swartzia montana, Scorpidium scorpioides,* and *Drepanocladus* sp. It also contained pieces of wood and other plant fragments.

In a letter to the writer Dr. Butler states that he was exhorted by Professor W. H. Lang not to give the same generic name to a recent and a fossil fungus. However, not being completely satisfied that the fungus figured in his text-figure 2 was a fossil, since it came from the amorphous peat overlying the glacial clay, he chose to assign it to a living genus under the designation of *Rhizophagus* sp. Because of the identity of the Alberta specimens with the Pleistocene material from the Minnesota sites, and furthermore the occurrence at Springfield of another species of the same genus from the early Pleistocene, there is no longer any doubt about the fossil nature of the group. Accordingly, I am describing it as a fossil genus under the name *Rhizophagites*, suggested by Dr. Butler.

Rhizophagites Rosendahl, gen. nov. Mycelium consisting of subdichotomously branched, more or less tortuous, nonseptate, thick-walled hyphae, with unilateral projections, pale yellow to light brown in color and varying in thickness from 6.5 to 20.7 μ, producing terminally ovate or short pyriform or subspherical, yellowish brown to dark brown vesicles, varying in size from 42 × 46 μ to 103 × 124 μ, with walls considerably thicker than the walls of the mature hyphae, vesicles at first in open communication with the hyphae, later becoming variously occluded by basal plugs or septa at the neck of the stalk or in the stalk or by a second wall forming around the contents, sometimes a second vesicle is formed within by proliferation from the stalk; contents made up of numerous granules, oil globules and a number of angular crystal-like bodies, vacuoles occasionally present.

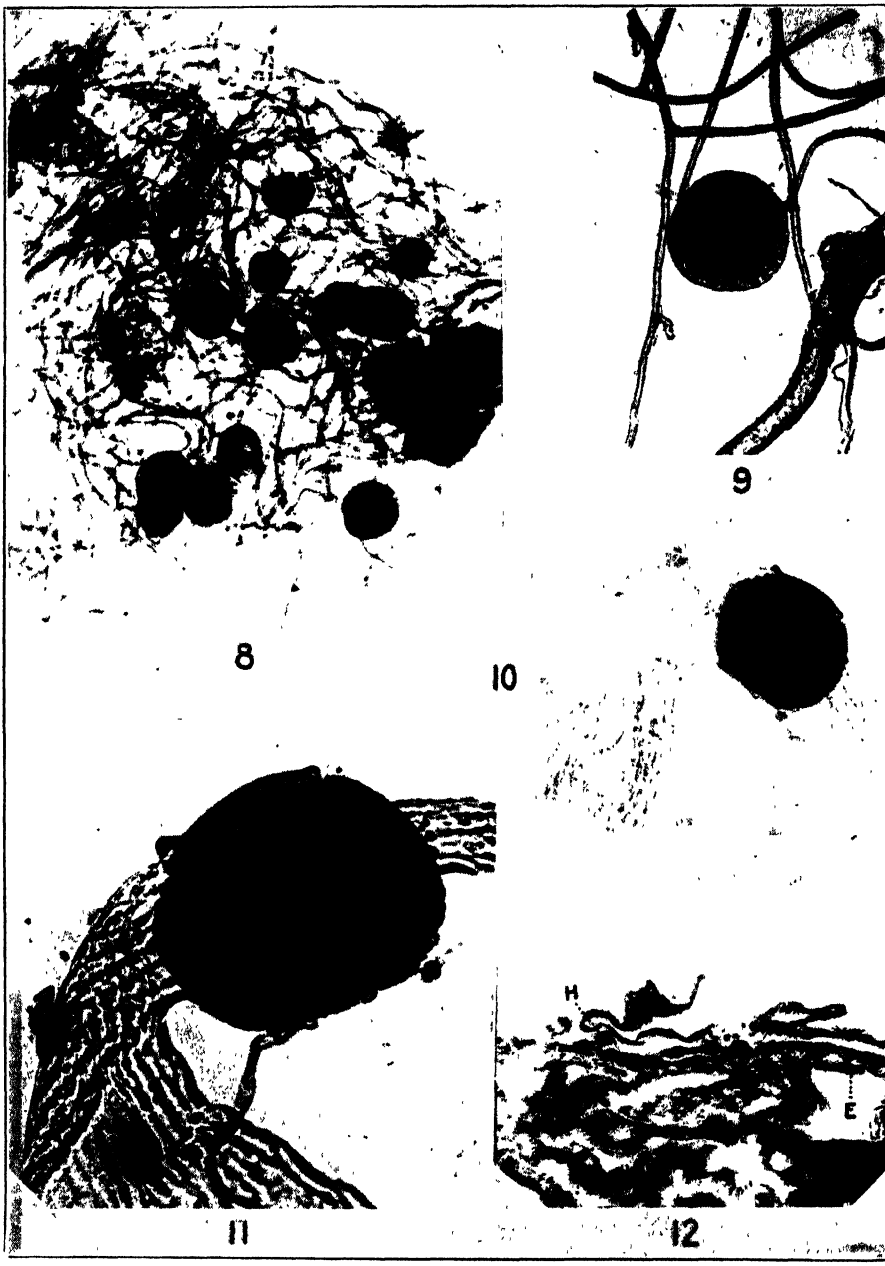
As here defined the genus consists of two species which may be distinguished as follows:

1. Vesicles light brown 75 × 79 μ to 103 × 124 μ, hyphae moderately tortuous, mostly 9–11 μ in diameter. *R. butleri.*
2. Vesicles dark brown 42 × 46 μ to 58 × 61 μ, hyphae very tortuous and irregular, 6.2–20.7 μ in diameter. *R. minnesotensis.*

Rhizophagites butleri Rosendahl, sp. nov. Hyphae moderately tortuous, with numerous unilateral projections and occasional diverticula, pale yellow in color, 9–11 μ in diameter and unform in thickness except where the branching occurs, stalks of the vesicles about the same diameter as the rest of the hyphae, vesicles chestnut-brown in color, oval to subspherical, varying in size from 75 × 79 μ to 103 × 124 μ, average size 89 × 98 μ, walls at the base of mature vesicles and walls of the neck of the stalks much thickened.

Rhizophagites minnesotensis Rosendahl, sp. nov. Hyphae very tortuous and with few unilateral projections, yellowish brown in color, uneven in thickness, varying from 6.2 to 20.7 μ in diameter, stalks of the vesicles thin and mostly elongated, vesicles dark brown in color, short pyriform to nearly spherical, varying in size from 42 × 46 μ to 58 × 61 μ, average size 48 × 53 μ, walls of mature vesicles not perceptibly thicker at the base.

The collections of the first species from the Alberta bogs and Moorhead, Minnesota, are of late Pleistocene origin, having apparently been deposited


8
9
10
11
12
H
E

in the silt of glacial lakes fronting the last ice sheet during its recession. The material from the deep wells at Bronson and Jackson dates back to the last interglacial interval. The collection of the second species is referable to early Pleistocene, being obtained from dense peat on the contact line between Cretaceous shale and Nebraskan till at Springfield, Minnesota.

In the same peat material from which the second species of *Rhizophagites* was obtained, well preserved fruiting bodies of another fungus were discovered. The first specimen found occurred free and consisted of a tangle of dark brown hyphae and fifteen circular perithecia (fig. 8). A second but smaller specimen was found attached to the tip of a moss plant (*Hypnum?*), but on account of the poor conditions of the temporary preparation it could not be determined whether any of the hyphae were in organic connection with the leaves and branches of the moss or were merely entangled in them. The dark brown circular fruiting bodies with a radiate cell structure and a central pore (figs. 9, 18) suggested that the organism belonged to the Microthyriaceae, and my inclination was to regard it as probably a fossil species of the genus *Microthyrium*, or in the event that the clusters of tangled hyphae belonged to the organism and represents free mycelia, then it might more properly be assigned to *Calothyrium*. On closer examination of the perithecia, however, it was discovered that they were not dimidiate but complete,[3] being provided with a well differentiated lower (fig. 19) as well as upper wall or membrane, the latter bearing a conspicuous central papilla with an apical pore (fig. 18). On account of the pressure to which they had been subjected under the load of glacial till they were very much flattened and in sectional view appear like a saucer with the central papilla rising slightly higher than the rim (figs. 12, 20). Except for the absence of asci and the dissolution of some of the delicate periclinal walls in both the upper and lower membranes the cell structure was found to be remarkably well preserved. Fungi with perithecia of this type have been segregated into the family Trichothyriaceae by Theissen (1914), and despite the fact

[3] I am indebted to Miss Louise Dosdall of the Division of Plant Pathology, University of Minnesota, for helpful suggestions in placing the fungus.

Explanation of figures 8–12

FIGS. 8–12. *Trichothyrites pleistocaenica*. FIG. 8. Cluster of perithecia with a tangle of hyphae most of which belong to a *Herpotrichia*-like form. (See text.) × 97. FIG. 9. Single perithecium more highly magnified. × 225. FIG. 10. Single perithecium on a moss leaf. Hyphae are shown faintly outlined on the surface of the leaf. × 205. FIG. 11. Same perithecium more highly magnified. × 415. FIG. 12. Cross section of spruce leaf showing two perithecia in vertical section. The one on the left is broken open along the right-hand margin. Epidermal cells of spruce leaf shown at E and fungal hyphae cross section at H. × 230.

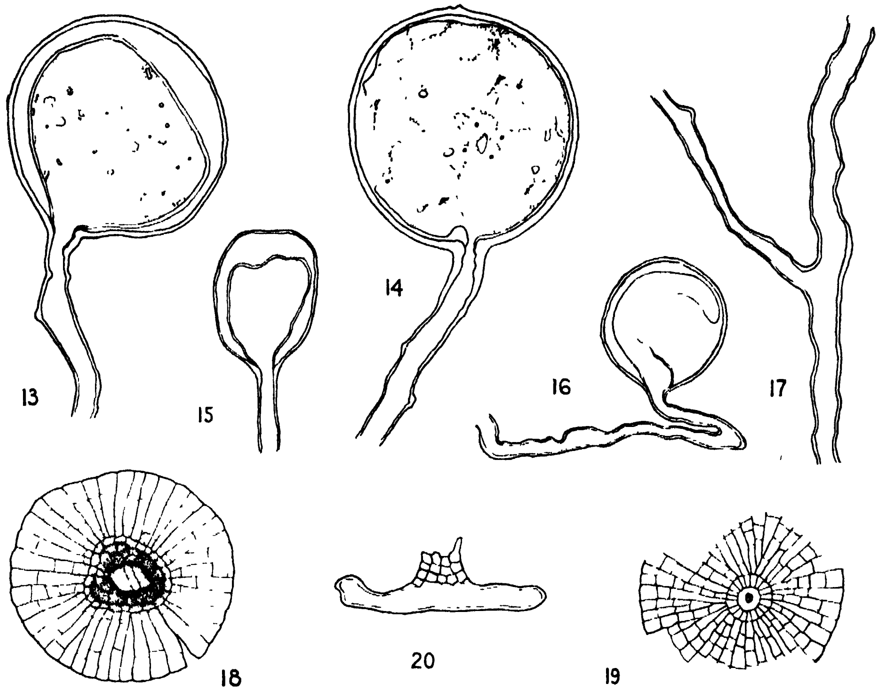
All the material for photo-micrograph figures 1–11 was prepared by mounting unstained in lactic acid and sealing the cover slips with Clarite. Figure 12 is from an unstained paraffin section. Wratten M plates and a Wratten medium yellow filter, together with a disc of daylight glass, were used in photographing.

that the living representatives of the family, so far as reported, occur almost wholly as parasites upon fungi of tropical flowering plants, the diagnostic characters set forth by Theissen would place the organism in this group. That it existed under cool or even cold conditions is clear from the fact that the peaty material from which it was recovered contained an abundance of spruce and tamarack needles, fragments of spruce wood and bark, and several species of mosses belonging mainly to the genera *Hypnum*, *Calliergon*, *Scorpidium*, *Camptothecium*, *Swartzia*, *Ditrichum*, and *Hylocomium*. *Swartzia montana*, which is characteristic of cold and subalpine places was encountered frequently and fruits of *Potamogeton* and achenes of two or three northern species of *Carex* were also fairly common in the plant debris.

Attempts were next made to connect the fungus with a possible host and to that end all the material was carefully re-examined. The first clue obtained was the discovery of patches of dark brown fungal hyphae on many of the spruce leaves. A few of these patches were removed and mounted, and it was found that they consisted of a thin weft of interlacing hyphae with denser knots at regularly spaced intervals. Also, in a few of the preparations the above mentioned circular fruiting bodies were found more or less enmeshed in the tangle of hyphae. Some of the spruce needles were thereupon imbedded in paraffin and cross sectioned, and it was revealed that the denser knots of the investing weft were situated directly above the stomata of the leaves, which explains their orderly arrangement in parallel rows observed in the free-hand preparations. These knots are composed of densely interwoven, crinkly hyphae and some of them attain considerable size and are nearly hemispherical in shape. The habit and structure suggest a species of *Herpotrichia*, but in the absence of really diagnostic characters the identity of the organism necessarily remains in doubt.

Sections that encountered the circular fruiting bodies showed these sometimes superimposed on the thin layer of investing hyphae (fig. 12) and occasionally over the knots, but in no case could any actual connection be made out between the perithecia and the underlying or contiguous hyphae. It is fairly certain that two different fungi are involved in the picture, but what relation, if any, they bear to each other is entirely problematic. In line with the reported fungicole habit of the group it is conceivable that the trichothyriaceous organism is parasitic upon the other fungus. However, doubt is thrown upon this assumption from the subsequent discovery of the actual attachment of hyphae and circular perithecia of the same organism to the stems and leaves of mosses (fig. 10) occurring in the deposit. Both in surface view and in cross sections the hyphae were found to be closely appressed to the leaves and stems of the mosses and there can scarcely be any doubt about the fungus vegetating upon the moss plants, but whether as a parasite or as a saprophyte it is obviously impossible to say. The mycelium

is sparse (fig. 10), the hyphae are all uniform, and there is no indication of another fungus being present on the moss as in the case of the spruce needles. Connections between the mycelium and the perithecia could not be demonstrated, although in figure 11 a hypha is shown still in contact with a perithecium.



FIGS. 13, 14. Vesicles of *Rhizophagites butleri* from the Moorhead and Bronson well sites respectively. Figure 13 shows a thick second wall formed around the contents and extending into the neck of the stalk. FIGS. 15, 16. Vesicles of *Rhizophagites minnesotensis*. FIG. 17. Hypha of same, showing variation in size and sub-dichotomous branching. FIGS. 18, 20. *Trichothyrites pleistocaenica*. FIG. 18. View of upper wall or membrane of perithecium showing radiate structure and central papilla with a definite ostiole. FIG. 19. Lower membrane, incomplete but with the central portion intact, showing a very regular radiate arrangement of the cells around a larger circular central cell. FIG. 20. Perithecium sectioned vertically but the section is to one side of the middle of the papilla. Note the small, thick-walled cells of the papilla and the finger-like process of one of the border cells of the ostiole.

All figures were drawn with the aid of camera lucida to a magnification of $\times 660$, reduced to half size in reproduction.

The perithecia from the moss and the spruce needles appear completely identical. They are the same in color, size, and every detail of structure, even to the trichome-like cells (fig. 20) that fringe the opening of the papilla, and I am convinced that they belong to the same species of fungus. The fact that the organism occurs on such widely divergent hosts as spruce leaves (or

another fungus on the spruce leaves) and at least two different species of mosses would indicate that it is a saprophyte, capable of living upon a variety of substrata in the litter of the Pleistocene bog. So far as it has been possible to ascertain, no existing fungus of this group has hitherto been reported from cool northern bogs, and the chances are that it represents an extinct species. There are several published reports of the occurrence of this general type of fungus during the Tertiary, ranging all the way from the Eocene to the Pliocene, and it is perhaps not without significance that at least three of the fossil finds were on needles of conifers. The first of the reports is by Pampaloni (1902), who described *Microthyrites dysodilis* from the Miocene of Sicily. Engelhardt and Kinkelin (1908), in their study of the upper Pliocene flora of the lower valley of the Main, reported the occurrence on *Ilex* leaves of a fungus with shield-shaped perithecia and a free mycelium which, on the interpretation of Dr. Möbius, they referred to *Asterina* (?) *ilicis* Ell. They pointed out, however, that because of the absence of spores the identification could not be considered as entirely certain. Their text-figure shows a perithecium with a slightly irregular margin and a small undifferentiated opening which suggests the absence of a true ostiole. They also found on *Buxus* leaves, in the same deposit, fruiting bodies of an Asterina-like fungus but without a free mycelium. Nathorst (1915) likewise referred doubtfully to *Asterina* a fungus obtained from cuticle preparations of leaves and twigs of *Sequoia langsdorfii* from the Tertiary of Elsmereland.

In his "Nachträge zur Tertiarflora Schlesiens" Kräusel (1920) recounted the finding of round, shield-shaped bodies, about 70 μ in diameter, in association with the leaves of *Sequoia langsdorfii*. On account of their being joined together by hyphal threads he concluded that these bodies belonged to a fungus, and he stated that they resembled in high degree the perithecia (*Gehäusen*) of the Microthyriaceae. He regarded them as being very closely similar to the form reported on *Ilex* leaves by Engelhardt and Kinkelin. It should be noted, however, that a perithecium illustrated by Kräusel has a definite ostiole, an entire margin, and is composed of fewer but relatively larger cells than the one shown in the illustration of Engelhardt and Kinkelin. According to Edwards (1922), Kräusel's material was of Miocene age.

Two years after the publication of Kräusel's paper, Edwards (1922) reported the discovery of a microthyriaceous fungus from the Eocene of Scotland. This too was obtained from conifer needles. The material ostensibly was in better shape than in the collections cited above, for it was described in much greater detail and was definitely disposed of as *Phragmothyrites eocaenica*. Edwards' photomicrographic illustration of a mature perithecium is strikingly like the figure of the fungus that Engelhardt and Kinkelin referred doubtfully to *Asterina ilicis* Ell., and the close similarity in the

structure of perithecia suggest that the two probably belonged in the same genus. The assignment to *Asterina ilicis* Ellis was unfortunate, however, since Theissen (1913) has subsequently shown that the latter belongs to the *Discomycetes*.

In all of these reports identification was apparently based only upon the surface view of the fruiting bodies, but since it is next to impossible to determine from the surface aspect alone whether the perithecia (ascomata) are dimidiate or complete, it is not certain that they all belong to the Microthyriaceae. Kräusel's illustration of one of the circular bodies found in his fossil material bears a very close resemblance to the perithecia of the Pleistocene fungus under discussion, and it is not improbable that the organisms involved are congeneric. Whether or not this is the case the Minnesota material can not be referred to any of the previously named fossils, and I am venturing to describe it as a fossil genus belonging to the Trichothyriaceae. The existing genera of the family are segregated upon spore characters, and since spores are entirely lacking in all the material seen it can hardly be treated otherwise than a form genus for which the name *Trichothyrites* seems the most appropriate.

Trichothyrites pleistocaenica Rosendahl, gen. et spec. nov. Mycelium[4] consisting of yellowish or brownish, branching, septate hyphae with occasional anastamoses, 5–6.7 μ in diameter, individual cells (20) 28–33 (41) μ long, perithecia dark brown to nearly black, circular or nearly so, disk-shaped, or because of slightly upturned margin shallow saucer-shaped, 70–95 μ in diameter, complete, with upper and lower membranes composed of radially arranged cells, upper membrane with a central papilla having a distinct pore or ostiole, marginal cells of membrane 4–5 μ wide, 6–8 μ long, cells of papilla more nearly quadrangular and thick walled, several of the marginal cells of pore prolonged into finger-like processes, cells of lower membrane all thin walled and radiating from a circular central cell, asci and spores lacking.

Found on leaves of Black Spruce in association with an unknown fungus and on two species of hypnaceous mosses, in an early Pleistocene deposit at Springfield, Minnesota.

DEPARTMENT OF BOTANY, UNIVERSITY OF MINNESOTA
MINNEAPOLIS, MINNESOTA

Literature Cited

Butler, E. J. 1939. The occurrence and systematic position of the vesicular-arbuscular type of mycorrhizal fungi. Trans. Brit. Mycol. Soc. **22**: 274–301.

Edwards, W. N. 1922. An Eocene microthyriaceous fungus from Mull, Scotland. Trans. Brit. Mycol. Soc. **8**: 66–72.

Engelhardt, H. & Kinkelin, F. 1908. Oberpliocäne Flora und Fauna des Untermainthales, insbesondere des Frankfurter Klärbeckens. Abh. Senckenb. Naturf. Ges. **29**: 149.

[4] Description of mycelium drawn from fungus on moss plants. On the spruce leaf materials it is obscured by the tangled hyphae of the other fungus present.

Kräusel, R. 1920. Nachträge zur Tertiärflora Schlesiens. Jahrb. Preuss. Geol. Landes. **39**: 329–417.

Leverett, Frank & Sardeson, Frederick W. 1932. Quaternary geology of Minnesota and parts of adjacent states. U. S. Geol. Survey, Prof. Paper 161. 1–149.

Nathorst, A. G. 1915. Tertiäre Pfanzenreste aus Ellesmere-Land. Rep. 2nd Norweg. Arctic Exped. in the "Fram," 1898–1902, 35: 3–16.

Pampaloni, L. 1902. Microflora e microfauna nel disodile Melilli in Sicilia. Atti Accad. Lincei **11**: 248–253.

Theissen, F. 1913. Die Gattung *Asterina*. Abh. Zool.-Bot. Ges. Wien **7**: 1–130.

————. 1914. Die *Trichothyriaceae*. Beih. Bot. Centralb. **32**: 1–16.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 2, pp. 139–151 MARCH, 1943

ASAHINA'S MICROCHEMICAL STUDIES ON THE CLADONIAE[1]

ALEXANDER W. EVANS

Asahina's microchemical studies on *Cladonia* (and other critical lichen-genera) have made it possible for the taxonomist to demonstrate the presence of numerous lichen-acids and allied substances without recourse to the complicated methods employed by the organic chemist. The results of these studies are given in several special articles and in two series of contributions: (1) *Lichenologische Notizen* (2, 8, 13),[2] the first number of which appeared in 1933; and (2) *Mikrochemischer Nachweis der Flechtenstoffe* (1, 3, 4, 5, 6, 7, 9, 10, 12, 15), the first number of which appeared in 1936. Of the first series fifteen numbers have been published; of the second, eleven. Of the special articles the following have a direct bearing on North American *Cladoniae: Ueber den Chemismus der Flechten der Cocciferae* (11); *Japanische Arten der Cocciferae* (13); *Cladonia verticillata Hoffm. und Cladonia Calycantha (Del.) Nyl. aus Japan* (17); and *Cladonia chlorophaea und verwandte Arten* (18).

Asahina's work up to 1938 has been reviewed by Sandstede in his supplement to Vainio's monograph on the *Cladoniae* (19), but there are few other references to it in the recent literature on lichens. It seems advisable, therefore, to bring to the attention of North American students the more important features of his methods and to summarize the results which he has already obtained. In doing this no attempt will be made to discuss the chemical structure of the various substances involved. Those interested in this aspect of the subject may consult Zopf's comprehensive study on lichen-substances (20) or Asahina's recent classification of these substances from a chemical standpoint (14).

In order to demonstrate the presence of a definite lichen-substance in a specimen Asahina's methods A and B (1, pp. 519, 520) are applicable in most instances. These methods involve two steps or processes. In the first step a portion of the lichen to be tested is placed on a slide and extracted by means of a volatile solvent, such as acetone or chloroform, applied drop by drop; and care must be taken to avoid an excess of the solvent, otherwise the solution will spread over too large an area. In the case of the *Cladoniae* either the primary squamules or the podetia may be investigated. If the

[1] Contribution from the Osborn Botanical Labortory.

[2] The numbers refer to the bibliography at the end of this paper. The only titles listed are those which refer, directly or indirectly, to species of *Cladonia* known to occur in North America.

podetia are small it may be necessary to use two or more, but if they are large a single podetium or even a portion of a podetium will be sufficient. Upon the evaporation of the solvent and the removal of the lichen-sample, a dry extract is left on the slide, usually in the form of a whitish or yellowish coating or crust, in which as a rule little of a definite nature can be distinguished under the microscope.

The material is now ready for the second step. This involves the use of a second solvent, from which the substance or some compound of the substance will crystallize out in a recognizable form. A drop or two of the solvent should be placed on the dry extract and a cover-glass applied. Then, in order to facilitate the solution it is usually necessary to apply a gentle heat, and Asahina recommends for this purpose a microflame, either of a gas burner or of an alcohol lamp. If care is taken, however, a lighted match may be sufficient. As the preparation cools the crystals gradually make their appearance. This may take place after a few minutes but may require an hour or more in the case of certain subtances. The solvents used in carrying out the second step include the following, designated by the abbreviations which Asahina employs (1, p. 519; 3, p. 860; 4, p. 529) :—

G.A.W., one part each of glycerine, alcohol, and water;
G.E., one part glycerine and three parts glacial acetic acid (Eisessig);
G.W.Py., one part glycerine, three parts water, and one part pyridine;
G.A.Q., two parts glycerine, two parts alcohol, and one part quinoline;
G.A.An., two parts glycerine, two parts alcohol, and one part aniline; and
G.A.o-T., two parts glycerine, two parts alcohol, and one part ortho-toluidine.

These various solutions, together with the acetone and the chloroform, should be kept in small bottles, the necks of which are closed with rubber medicine-droppers. By this means the reagents may be applied drop by drop, and the danger of adding an excess can be avoided.

Although most of the substances to be tested for are readily soluble in cold acetone, a few require hot or even boiling acetone before they can be brought into solution. Since acetone is inflammable and boils at a relatively low temperature (about 56° C) the heat must be carefully applied. Asahina (4, p. 530) recommends for this purpose a glass tube about 10 cm. long and 8 mm. in diameter. The lower end of this tube is gradually narrowed to a diameter of about 2 mm., and the narrowed portion is curved back in such a way that it lies parallel with the main tube, except at the free end, which is curved outward. This apparatus thus resembles, as Asahina points out, a miniature burette of the Gay Lussac type (see 4, *f. 33–35*). The lichens or lichen-fragments to be extracted are pressed down into the tube, covered with acetone, and heated over a microflame. In doing this the tube should be held obliquely and care should be taken not to expel the contents by applying the heat too abruptly. After the acetone has boiled gently for a minute or

two the contents of the tube should be poured out through the narrow end upon a slide and allowed to evaporate to complete dryness. The extract thus obtained, which tends to spread out over a considerable surface, should be scraped together by means of a scalpel before proceeding to the second step in Asahina's method of crystallization.

The crystals of certain lichen-substances are large enough to be recognized under the low power of the microscope, but the high power is necessary in most cases to bring out their distinctive features. There are a few substances, in fact, in which the crystals are so very minute that they can be easily overlooked. If the presence of a given substance is suspected in a lichen and if negative results are obtained at the first trial, a second or even a third extraction may be advisable before deciding that the substance is absent. It must be kept in mind also that the presence of certain substances may make the demonstration of other substances by microchemical methods difficult if not impossible.

At the present time 19 lichen-acids and related substances, which can be demonstrated by Asahina's methods, have been reported in the *Cladoniae*. These substances, which are arranged below in alphabetical sequence, will now be considered with respect to the following data: (1) the distribution of the substance among the various North American species of the genus; (2) the reagents to be used in its demonstration; and (3) the characteristic features of the crystals obtained. In this resumé many of the reactions described by Asahina are omitted and the attempt is made to emphasize those of the most practical importance from the standpoint of the taxonomist. Additions to the list will doubtless be made in the near future.

1. Atronorine. This substance is widely distributed among the lichens and has been reported in the following species of *Cladonia*: *C. caespiticia* (Pers.) Floerke, *C. cariosa* (Ach.) Spreng., *C. Evansii* des Abbayes, *C. furcata* (Huds.) Schrad., *C. gracilis* (L.) Willd. var. *elongata* (Jacq.) Floerke, *C. major* (Hag.) Sandst., *C. papillaria* (Ehrh.) Hoffm., *C. rangiferina* (L.) Web., *C. rangiformis* Hoffm., and *C. symphycarpia* Floerke. It will be noticed that none of these species are red-fruited. Atronorine is negative with P[3] but gives a pale lemon color with K, very different from the deep yellow produced by thamnolic acid. In species with persistent primary squamules the reaction with K shows particularly well if the reagent is applied to the chalky lower surface.

Perhaps the best way to demonstrate atronorine microchemically is to extract the lichen-sample with acetone and to apply the G.A.o-T. solution to the dry residue. If the preparation, after careful heating, is examined under the microscope slender yellow crystals are soon seen to make their

[3] The abbreviation "P" stands for paraphenylenediamine, the abbreviation "K," for potassium hydroxide.

appearance (see Asahina, 4, p. 535, *f. 13, pl. 2, f. 6*). These are in the form of very narrow plates with parallel sides and may present the appearance of needles if seen on edge. The crystals, if occurring singly, are usually variously curved or contorted and show more or less irregular branching at their ends. They are most characteristic, however, when they form radiating clusters. Under these circumstances the crystals tend to branch repeatedly at their free ends and to give rise to intricately interwoven clusters of thread-like elements. Another excellent method of demonstrating atronorine is by treating the dry acetone extract with a saturated solution of barium hydroxide (3, p. 961, *f. 15*). After heating gently the barium salt crystallizes out in the form of dense spherical clusters of delicate yellow lamellae, which look like fine needles if examined casually.

2. Baeomycic acid. This acid, which was first isolated from *Baeomyces roseus* Pers., has been found by Asahina in a single species of *Cladonia*, *C. strepsilis* (Ach.) Vainio (9, p. 652), and is responsible for the yellow color which this species shows upon treatment with P. The pure acid yields characteristic crystals with various reagents and the same results can be obtained with the acetone extract of the *Baeomyces*. The G.A.Q. solution, for example, brings about the formation of minute, very pale yellow, thin rhomboidal plates, occurring singly or in irregular groups. In some cases, as shown by one of Asahina's figures (9, *f. 84*) the ends of the rhombi are shortly truncate, but the majority are regularly formed (9, *pl. 5, f. 3*). The presence of strepsiline, unfortunately, which accompanies the baeomycic acid in *C. strepsilis*, interferes with its crystallization, and Asahina gives no method by means of which the strepsiline can be first separated.

3. Barbatic acid. Barbatic acid was first extracted in 1880 from material which had been determined as *Usnea barbata* (L.) Wigg., but the identity of this material is still in doubt. At a later date Zopf (20, p. 238) reported the occurrence of the acid in several other lichens, including *U. ceratina* Ach. and *Alectoria ochroleuca* (Ehrh.) Nyl. Asahina (3, p. 870) has shown, however, that the acid present in these two species is not barbatic acid but diffractic acid, a substance first isolated from the Japanese *U. diffrata* Vainio. The distribution of barbatic acid, therefore, among the species of *Usnea* and *Alectoria* awaits further investigation. In the genus *Cladonia* barbatic acid has been reported as a definite component of the following species (see 11, p. 24): *C. amaurocraea* (Floerke) Schaer., *C. bacillaris* (Ach.) Nyl., *C. coccifera* (L.) Willd., *C. cristatella* Tuck., *C. didyma* (Fée) Vainio, *C. Floerkeana* (Fr.) Floerke, and *C. macilenta* Hoffm. It will be noted that all of these species, with the exception of *C. amaurocraea*, are members of the section *Cocciferae*. Barbatic acid, as shown by Asahina (3, p. 868, and 5, p. 856), is indistinguishable from the coccelic acid of Hesse and from a substance distinguished by Zopf (21, p. 55) under the name

cenomyceine. Both of these substances were listed by Zopf under most of the species enumerated above.

For the demonstration of barbatic acid, which is not difficult, either the G.E. solution (3, p. 868) or the G.W.Py. solution (5, p. 856) may be applied to the dried acetone extract. If the G.E. solution is used the acid, after gentle heating, will appear in the form of short, refractive, colorless rhombic prisms or rectangular lamellae (3, *f. 27*), associated in some cases with boat-shaped prismatic structures having pointed ends (5, *pl. 5, f. 3*). The crystals obtained by means of the G.W.Py. solution, likewise after careful heating, are perhaps even more satisfactory. These crystals are in the form of colorless, narrow, four-sided lamellae (5, *f. 11, pl. 5, f. 1*). In their most typical condition they are oblique at the ends and rhombic in outline, but the ends may be square or angled, in the latter case showing a combination of the oblique and square conditions. The most characteristic crystals, however, are united in pairs, and it is usual for one or both members of the pair to project beyond the line of junction. Twin crystals of this type can readily be found in most preparations and are particularly striking if the line of junction is relatively short and if the crystals project in opposite directions.

4. Bellidiflorine. Zopf, who isolated bellidiflorine from the northern *Cladonia bellidiflora* (Ach.) Schaer. in 1907 (20, p. 332), was unable to find it in any other member of the genus (21, p. 108). Asahina, however, demonstrated its presence in the following North American species, all belonging to the section *Cocciferae* (11, p. 24; 14, p. 603): *C. digitata* (L.) Hoffm., *C. deformis* Hoffm., *C. endoxantha* Vainio, *C. gonecha* (Ach.) Asahina (a recent segregate from *C. deformis*), *C. incrassata*,[4] *C. leporina* Fr. (13, p. 604), *C. macilenta*, *C. pleurota* (Floerke) Schaer., and *C. polydactyla* Floerke. In a few of the species bellidiflorine occurs only as an "accessory" substance, i.e., it is not invariably present.

Bellidiflorine dissolves with difficulty in cold acetone but readily passes into solution if the solvent is boiled. The method described on page 140 should therefore be employed. If the dried extract thus prepared is treated with the G.A.An. solution and gently heated (10, p. 771), the very characteristic crystals of the aniline salt are obtained. These crystals do not make their appearance immediately but only after a considerable time. They are in the form of minute, six-sided lamellae (10, *f. 99, pl. 6, f. 1*), which show a brownish yellow or brownish green color. In most cases the sides of the hexagons are equal, but some irregularity is to be expected.

5. Cryptochlorophaeic acid. According to our present knowledge this acid is confined to *Cladonia cryptochlorophaea* Asahina, a recent segregate from *C. chlorophaea* (Floerke) Spreng. (see 18, p. 710).

---

[4] The authorities for specific names are given only when the species are first mentioned.

The dry extract obtained by treating podetia of *C. cryptochlorophaea* with acetone is abundant, somewhat opaque, and more or less tinged with yellowish or brownish in transmitted light. It consists in most cases of several concentric bands and shows at the periphery a series of rounded projections. If the G.A.W. solution and gentle heat are applied to the extract the preparation forms upon cooling the characteristic colorless crystals of cryptochlorophaeic acid, which are in the form of long and exceedingly fine needles. When these occur singly they tend to be more or less curved, and both extremities become repeatedly subdivided. It is more usual, however, for the crystals to be arranged in dense, radiate clusters around a central point (18, *pl. 1, f. 1*). Under these circumstances they remain undivided at their attached ends but branch repeatedly at their free ends, the branches becoming finer and finer. In this way circular aggregates of crystals may be formed. These bear a certain resemblance to the crystal-aggregates which atronorine forms in the G.A.o-T. solution, but the latter are distinctly yellow, their larger elements are in the form of narrow bands, and their finer branches tend to be more intricately interwoven and distorted.

6. DIDYMIC ACID. Asahina announced the discovery of didymic acid in 1939 (11, p. 32) and demonstrated its presence in the following North American species of *Cladonia*, all belonging to the section *Cocciferae*: *C. cristatella*, *C. didyma*, *C. leporina*, and *C. vulcanica* Zolling. A short time later he added *C. incrassata* to the list (12, p. 467) and showed that his didymic acid was identical with the incrassatic acid of Zopf. The species in which didymic acid has so far been found are all members of the section *Cocciferae*.

The acid is readily soluble in acetone, and distinctive crystals are obtained if the dried extract is treated with the G.E. solution and gently heated. It is advisable to use for this purpose a sufficiently large lichen-sample. The crystals, which gradually appear after cooling, are colorless and in the form of long and narrow rhombic lamellae with oblique ends (12, *f. 100*). Many of the crystals, if seen on edge, present the appearance of needles, slightly thicker in the middle and tapering to long points. The crystals occur singly, in irregular groups, or in radiate or penicillate clusters (12, *pl. 1, f. 1*). Excellent results may be obtained also if the extract is similarly treated with the G.A.W. solution. The crystals resulting from this treatment are similar to those just described (12, *pl. 1, f. 2*) but, in the writer's experience, even more slender and needle-like. Radiate clusters of these crystals are frequent, although irregular groups and single crystals also occur abundantly. Asahina emphasizes the fact that the crystals may be curved or hook-like at the ends. He figures also abnormal S-shaped crystals with the ends variously subdivided (12, *f. 101*).

7. FUMARPROTOCETRARIC ACID. Zopf (20, p. 173) notes the occurrence of this bitter substance in several genera of the lichens, but it seems to be espe-

cially widely distributed in the genus *Cladonia*. Even here, however, it is restricted to the subgenus *Cladina* and the subsections *Chasmariae* and *Clausae*. It is therefore lacking in all red-fruited species and in the subsection *Unciales*. Fumarprotocetraric acid may be regarded as the characteristic acid, or as one of the characteristic acids, in the following North American species: *C. borbonica* (Del.) Nyl., *C. caespiticia*, *C. calycantha* Del. (16, p. 469), *C. chlorophaea*, *C. clavulifera* Vainio, *C. coniocraea* (Floerke) Spreng., *C. conista* (Ach.) Robbins, *C. cornutoradiata* (Coem.) Sandst., *C. fimbriata* (L.) Fr., *C. furcata* (Huds.) Schrad., *C. gracilis*, *C. major*, *C. mateocyatha* Robbins, *C. mitrula* Tuck., *C. multiformis* Merrill, *C. pityrea* (Floerke) Fr., *C. pyxidata* (L.) Hoffm., *C. rangiferina*, *C. scabriuscula* (Del.) Leight., *C. sylvatica* (L.) Hoffm., *C. tenuis* (Floerke) Harm., and *C. verticillata* (Hoffm.) Schaer. It occurs also, as an accessory substance, in *C. cryptochlorophaea*, *C. Grayi* Merrill, *C. merochlorophaea* Asahina, and *C. nemoxyna* (Ach.) Nyl.

For the demonstration of fumarprotocetraric acid the negative reaction with K and the distinctly red color produced by P are usually sufficient. If, for any reason, doubt should arise Asahina's microchemical methods may be employed. He recommends, in the case of *C. furcata*, for example (9, p. 659), the extraction by acetone diluted with 15 per cent of water. The material should be boiled in this mixture and the dried extract should be treated with the G.A.An. solution. After careful heating and subsequent cooling the aniline compound will crystallize out in the form of long and fine yellow needles, variable in length and arranged in radiating cluster. These as a rule do not form complete circles but show the needles distributed in two or more sectorial groups.

8. Grayanic acid. This acid represents the characteristic constituent of *C. Grayi*, as now defined by Asahina (see 18, p. 713), and occurs also in *C. borbonica* (18, p. 717). When Asahina first extracted grayanic acid he considered it identical with the chlorophaeic acid of Zopf (12, p. 468) but apparently now regards the latter as an impure substance.

If a podetium of *C. Grayi* is treated with acetone the dried extract already shows definite, needle-like, colorless crystals of grayanic acid. At the periphery of the preparation these usually occur in spreading or radiating groups, but in many cases they are free from one another and irregularly scattered (12, *pl. 1, f. 3*). In cases of doubt the application of the G.A.W. solution, followed by gentle heating, will bring about the appearance of longer and exceedingly fine needles, forming definite radiate clusters or irregular groups (12, *pl. 1, f. 5*).

9. Homosekikaic acid. Asahina first produced this acid synthetically and then demonstrated its presence in Japanese material of *C. pityrea* (7, p. 249). It is apparently an accessory substance in this species, since it has

not yet been found in European or North American specimens. In *C. nemoxyna,* however, homosekikaic acid is the characteristic substance present and is identical, as Asahina soon showed, with the nemoxynic acid of Zopf (8, p. 251).

In order to prove that homosekikaic acid is present Asahina's directions (7, p. 250) should be carefully followed. The dried acetone extract, as he points out, presents a varnish-like appearance, and he directs that this extract should be scraped together into a compact mass. To this a cover-glass smeared with the G.A.o-T. solution should be directly applied. If the preparation is then studied, without heating, under the microscope, one or more yellowish oily masses will soon be seen to make their appearance and in these the crystals of the ortho-toluidine salt will quickly be visible. These are in the form of exceedingly thin hexagonal plates, which occur singly or in lamellate clusters (7, *pl. 1, f. 6*). The sides of an individual plate are, in most cases, unequal in length.

10. MEROCHLOROPHAEIC ACID. At the present time this acid is known only in *C. merochlorophaea,* a recent segregate from *C. chlorophaea* (18, p. 710). A sufficient amount of extract for testing can usually be obtained if a single podetium of *C. merochlorophaea* is treated with acetone, but two or more may be necessary if the podetia are unusually small. The extract presents a varnish-like appearance, and Asahina (18, p. 712) recommends further treatment with the G.E. solution, followed by gentle heating and subsequent cooling. The crystals which now appear usually radiate out irregularly from a central area and are in the form of thin colorless lamellae, with parallel sides and oblique ends, the acute angles of which measure about 50°. The angles of course appear less if the lamellae do not lie flat, and the crystals may look like needles if seen on edge.

11. NORSTICTIC ACID. This name was given by Asahina and Yanagita to a substance obtained from *Lobaria pulmonaria* (L.) Hoffm. (9, p. 655). It has since been found in *Parmelia acetabulum* (Neck.) Duby, in *Usnea japonica* Vainio, and in *Cladonia subcariosa* Nyl. The acid is responsible for the deep red color which the *Cladonia* shows upon the application of K.

Norstictic acid is readily soluble in acetone, and perhaps the easiest way to demonstrate its presence microchemically is to treat the dried extract with a solution of potassium carbonate in the presence of K. Asahina recommends for this purpose a 10 per cent solution of K_2CO_3 plus a 5 per cent solution of KOH. The potassium salt will then appear, especially after heating, in the form of short straight needles, yellowish red to red in color. These occur either separately or variously grouped and may form radiate clusters. Another solution which gives excellent results is the G.A.o-T. solution. If this is added to the dry extract pale yellow crystals will appear, especially after heating, in the form of exceedingly thin, four angled lamellae (9, *f. 90*), occurring singly or in irregular groups.

12. Perlatolic acid. This substance, first extracted by Asahina and Fujikawa from *Parmelia cetrarioides* Del. var. *typica* DR. (6, p. 40), has recently been demonstrated also in two North American species of *Cladonia*, *C. Evansii* and *C. impexa* Harm. (15, p. 186, 189). The acid can be readily detected by treating the dry acetone extract with the G.A.Q. solution, followed by gentle heating. Upon cooling the characteristic crystals will appear, in some cases only after several hours, in the form of dense radiating clusters of colorless, exceedingly fine straight needles (15, *f. 3*). As a rule only one or a very few such clusters are present in a single preparation.

13. Psoromic acid. Although widely distributed among lichens in general (20, p. 198) psoromic acid has been reported from very few species of *Cladonia*. At the present time, in fact, *C. alpicola* (Flot.) Vainio and *C. alpestris* (L.) Rabenh. f. *aberrans* des Abbayes are the only North American forms that can be definitely cited from the literature (21, p. 87; 2, p. 804; 9, p. 656; 15, p. 190).

Lichens containing psoromic acid are negative or nearly so with K but give a deep yellow color with P. Extraction with acetone takes place readily, and if the dried residue is treated with the G.E. solution and gently heated the psoromic acid will crystallize out upon cooling in the form of penicillate or radiate clusters of fine colorless needles (9, *f. 52*). As Asahina points out these clusters may be large enough to be visible with the naked eye.

14. Squamatic acid. This substance is apparently restricted to the *Cladoniae*. It was first extracted from *C. squamosa* (Scop.) Hoffm. but is now known also in the following additional North American species (21, p. 106; 11, p. 24): *C. bellidiflora*, *C. caespiticia*, *C. cenotea* (Ach.) Schaer., *C. crispata* (Ach.) Flot., *C. delicata* (Ehrh.) Floerke, *C. glauca* Floerke, *C. gonecha*, *C. incrassata*, *C. strepsilis*. It may be noted that some of these species are red-fruited and others brown-fruited.

Since squamatic acid is only slightly soluble in cold acetone but more readily so in hot acetone, Asahina's burette-like tube is advisable for its extraction. If the residue thus obtained is treated with the G.E. solution and gently heated, the acid will crystallize out upon cooling in the form of minute, colorless, rhombic plates or truncated, rhombic, double pyramids (6, *f. 58*). In many cases small groups of crystals coalesce in various ways and thus form irregular compound crystals. The red-fruited species listed above contain usnic acid as well as squamatic acid, and Asahina recommends in such cases the use of the G.A.An. solution. In this solution the aniline salt of squamatic acid appears in the form of colorless rhombic prisms (10, *f. 99*).

15. Stictic acid. The extraction of stictic acid from *Lobaria pulmonaria* (*Sticta pulmonaria* Ach.) was made nearly a hundred years ago (20, p. 204), and the substance has since been found in the genera *Parmelia*, *Ramalina*, and *Stereocaulon* (7, p. 655). Although there are no reports in the literature

of its occurrence in the genus *Cladonia*, Asahina (in a recent letter) notes its presence in one of the North American species. It is accompanied by norstictic acid, and he has already pointed out that these two acids are not infrequently produced by the same species (7, p. 655). Since Asahina has not yet published his observations on the *Cladonia* in question no further details can be given here.

The demonstration of stictic acid follows a familiar pattern. The lichen-sample is first extracted with acetone, and the residue left after evaporation is treated with the G.A.o-T. solution and carefully heated. Upon cooling characteristic crystals make their appearance. They are in the form of exceedingly thin, hexagonal lamellae, the sides of which in most cases are equal (7, *f. 89*). According to Asahina the crystals are yellow, but the color may be so pale that they appear colorless. The crystals occur singly or in indefinite overlapping groups, and the surface shows a series of irregular lines or other markings.

16. STREPSILINE. This substance, according to our present knowledge, is confined to *C. strepsilis*. When the squamules or podetia of this species are treated with chloride of lime a more or less distinct green or bluish green color is produced, and students of the genus have regarded this color as a proof that strepsiline was present. Asahina's microchemical methods, however, give more trustworthy results, since the color-reaction is not always clear. He directs (12, p. 469) that the specimen to be tested should be extracted with acetone and that the residue obtained after drying should be treated with the G.E. solution and carefully heated. Upon cooling the crystals of the strepsiline gradually make their appearance. These crystals are colorless and minute and in some cases very scantily produced. They are therefore easily overlooked and it may be necessary to make two or more extractions before a successful demonstration is obtained. The crystals (20, *f. 58;* 12, *pl. 1, f. 6*) are in the form of rhombic plates, which may, if sufficiently thick, show a pale brownish tint. The acute angles of the rhombic faces measure 68°, and the surface is usually marked with a series of fine parallel lines. The crystals occur singly or unite to form compound crystals of various forms. The most characteristic of these appear split at one or both ends, with the free portions diverging from each other.

17. THAMNOLIC ACID. This acid derives its names from *Thamnolia vermicularis* (Sw.) Ach., in which it was first found. It is now known to occur also in several other lichen-genera and in the following North American species of *Cladonia* (9, p. 651; 10, p. 768; 11, p. 24): *C. delicata*, *C. digitata*, *C. endoxantha*, *C. macilenta*, *C. polydactyla*, *C. Ravenelii* Tuck., *C. santensis* Tuck. (*C. persquamulosa* Merrill), and *C. subsquamosa* Nyl. The red-fruited species in this list belong to the subsection *Subglaucescentes;* the brown-fruited, to the subsection *Chasmariae*. Several other species, not yet recorded in the literature, will probably be added to the list in the near future.

The presence of thamnolic acid is shown by the bright yellow color produced by K, together with the deep orange or red color produced by P. To demonstrate the acid microchemically extraction with hot acetone is advisable, since cold acetone is almost inactive as a solvent. For further treatment the G.A.An. solution (9, p. 651) is especially to be recommended. This should be added drop by drop to the dry residue and careful heat applied. The preparation will then assume a deep yellow color, accompanied by the production of bubbles of CO_2, and characteristic crystals will make their appearance upon cooling. These are in the form of fine yellow needles, grouped together in dense radiate or fasciculate clusters (9, *pl. 5, f. 1*).

18. USNIC ACID. As the name implies usnic acid was first demonstrated in the genus *Usnea*. Now, however, it is recognized as one of the most widely distributed of the lichen-acids, and Zopf (20, p. 102) notes its occurrence in nine distinct families. In the genus *Cladonia* the acid represents the characteristic substance or one of the characteristic substances in the following North American species (21, p. 106; 11, p. 24): *C. alpestris, C. impexa, C. mitis* Sandst., *C. sylvatica*, and *C. tenuis*, representing the subgenus *Cladina; C. bellidiflora, C. coccifera, C. cristatella, C. deformis, C. gonecha, C. incrassata, C. leporina*, and *C. pleurota*, representing the subsection *Stramineo-flavidae* of the section *Cocciferae; C. amaurocraea, C. Boryi* Tuck., *C. caroliniana* (Schwein.) Tuck., and *C. uncialis* (L.) Web., representing the subsection *Unciales; C. foliacea* (Huds.) Willd.[5] and *C. cyanipes* (Sommerf.) Vainio, representing the groups *Foliosae* and *Ochroleucae*, respectively, of the subsection *Clausae*. It occurs also, as an accessory substance, in *C. bacillaris* and *C. Floerkeana*, representatives of the subsection *Subglaucescentes* of the section *Cocciferae* (13, p. 603). It will be seen that the foregoing list includes no representatives of the large subsection *Chasmariae* or of the large groups *Podostelides* and *Thallostelides* of the subsection *Clausae*.

Lichens containing usnic acid tend to show a more or less marked yellowish tinge, although this is by no means invariably the case. They are negative with both K and P (unless certain other acids are present also), but turn distinctly yellow with chloride of lime, especially in the presence of K. The extraction of the acid for microchemical study can be made with either acetone or chloroform, but the latter is perhaps preferable because it leaves certain other lichen-substances undissolved. The extract obtained from either solvent is pale yellow and crystalline in appearance. Further treatment, however, is necessary in order to produce satisfactory crystals of the acid and for this purpose the G.E. solution yields excellent results (3, p. 863). After careful heating and subsequent cooling these crystals gradually make their appearance and can readily be seen under the low power. They are in

[5] The occurrence of the true *C. foliacea* in North America is open to question, but a closely allied species is not infrequent.

the form of yellow needles or narrow lamellae with parallel sides, the ends of which are obliquely cut off or taper to long points. The crystals occur singly, in indefinite groups, or in loose radiating clusters (3, *f. 17*).

19. ZEORINE. Zeorine was first extracted from some species of *Zeora*, which is regarded at the present time as a synonym of *Lecanora*. It is now known also in various other genera of the Lecanoraceae, in two genera of the Physciaceae (20, p. 53), and in two red-fruited species of *Cladonia, C. deformis* and *C. pleurota*. If a podetium of one of these species is extracted with acetone, a residue is left which yields characteristic crystals upon further treatment with the G.A.An. solution (10, p. 770). As in other cases heat should be carefully applied to the preparation, which should then be allowed to cool. The crystals (10, *f. 97*) are minute, colorless, and highly refractive. The most typical are in the form of truncated, hexagonal, double pyramids. If such a crystal is viewed from above it shows a regular hexagonal outline, and a second hexagon can be distinguished at a higher level by careful focusing. Other crystals are in the form of complete, broad or narrow, hexagonal pyramids, and the latter not infrequently show a broader equatorial band. In some cases the sharply angled crystals are accompanied by irregular crystals in which the angles are rounded or otherwise indistinct.

Microchemical methods for the detection of certain lichen-substances found in the *Cladoniae* have not yet been described and may not be applicable. These include the following: cervicornic acid, found in the brown apothecia of certain forms of *C. verticillata* (21, p. 84); destrictic acid, found in the apothecia and spermagonia of the European *C. destricta* Nyl. (20, p. 331); fimbriatic acid, found in *C. fimbriata* and *C. major* (20, p. 107); rangiformic acid, found in *C. mitis* (19, p. 91) and *C. rangiformis* (21, p. 106); and rhodoclonic acid, found in the apothecia of the red-fruited species (21, p. 55).

Asahina's microchemical investigations afford a new method of attack for the taxonomist by enabling him to determine many chemical features of lichens with comparative ease. They do not settle, however, the controversy regarding the significance of chemical differences from a taxonomic standpoint. Some writers regard such differences, if constant, as important as morphological differences; others assign them a secondary value and accept them only when supported by morphological differences; still others consider them of no taxonomic significance whatever. Which of these views will ultimately prevail must be left for the future to decide.

YALE UNIVERSITY
NEW HAVEN, CONNECTICUT

Literature Cited

1. **Asahina, Y.** Mikrochemischer Nachweis der Flechtenstoffe (I). Jour. Jap. Bot. **12:** 516–525, *f. 1–11.* 1936.

2. ——— ———. Lichenologische Notizen (VIII). Jour. Jap. Bot. **12:** 802–809, *f. 47–50.* 1936.
3. ———————. Mikrochemischer Nachweis der Flechtenstoffe (II. Mitteil.). Jour. Jap. Bot. **12:** 529–536, *f. 12–32.* 1936.
4. ———————. Mikrochemischer Nachweis der Flechtenstoffe (III. Mitteil.). Jour. Jap. Bot. **13:** 529–536, *f. 33–43, pl. 2.* 1937.
5. ———————. Mikrochemischer Nachweis der Flechtenstoffe. IV. Mitteilung. Jour. Jap. Bot. **13:** 855–861, *f. 44–49, pl. 5.* 1937.
6. ———————. Mikrochemischer Nachweis der Flechtenstoffe. V. Mitteilung. Jour. Jap. Bot. **14:** 39–44, *f. 50–59, pl. 1, 2.* 1938.
7. ———————. Mikrochemischer Nachweis der Flechtenstoffe. VI. Mitteilung. Jour. Jap. Bot. **14:** 244–250, *f. 60–69, pl. 4.* 1938.
8. ———————. Lichenologische Notizen (X). Jour. Jap. Bot. **14:** 251–255, *f. 57–60.* 1938.
9. ———————. Mikrochemischer Nachweis der Flechtenstoffe. VIII. Mitteilung. Jour. Jap. Bot. **14:** 650–659, *f. 81–95, pl. 5.* 1938.
10. ———————. Mikrochemischer Nachweis der Flechtenstoffe. IX. Mitteilung. Jour. Jap. Bot. **14:** 467–473, *f. 96–99, pl. 6.* 1938.
11. ———————. Ueber den Chemismus der Flechten der *Cocciferae* (*Cladonia* subg. *Cenomyce*). Jour. Jap. Bot. **15:** 22–36, *f. 1–2.* 1939.
12. ———————. Mikrochemischer Nachweis der Flechtenstoffe. X. Mitteilung. Jour. Jap. Bot. **15:** 465–472, *f. 100–101, pl. 1.* 1939.
13. ———————. Japanische Arten der *Cocciferae* (*Cladonia-Coenomyce*). Jour. Jap. Bot. **15:** 602–620, 663–671, *f. 1–3, pl. 3–6.* 1939.
14. ——————— Flechtenstoffe. Fortschr. Chem. Organ. Nahrstoffe **2:** 27–60. 1939.
15. ———————. Mikrochemischer Nachweis der Flechtenstoffe. XI. Mitteilung. Jour. Jap. Bot. **16:** 185–193, *f. 1–10.* 1940.
16. ———————. *Cladonia verticillata* Hoffm. und *Cladonia calycantha* (Del.) Nyl. aus Japan. Jour. Jap. Bot. **16:** 462–470, *f. 1–3.* 1940.
17. ———————. Lichenologische Notizen (XIII). Jour. Jap. Bot. **16:** 517–522, *f. 66–68.* 1940.
18. ———————. Chemismus der *Cladonien* unter besonderer Berücksichtigung der japanischen Arten. 1. *Cladonia chlorophaea* und verwandte Arten. Jour. Jap. Bot. **16:** 709–727, *f. 1–6, pl. 1.* 1940.
19. **Sandstede, H.** Ergänzungen zur Wainio's "Monographia *Cladoniarum* universalis" unter besonderer Berücksichtigung des Verhaltens der *Cladonien* zu Asahina's Diaminprobe. Repert. Spec. Nov. Beih. **103:** 1–103. *pl. 1–16.* 1938.
20. **Zopf, W.** Die Flechtenstoffe in chemischer, botanischer, pharmakologischer und technischer Beziehung. i–xi, 1–450. *f. 1–71.* Jena, 1907.
21. ———————. Beiträge zu einer chemischen Monographie der *Cladoniaceen.* Ber. Deuts. Bot. Ges. **26:** 51–113, *f. 1–2, pl. 1–4.* 1908.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 152–163 MARCH, 1943

OBSERVATIONS ON THE CULTURE OF HEMITRICHIA VESPARIUM, WITH SPECIAL REFERENCE TO ITS BLACK PLASMODIAL COLOR

RUTH N. NAUSS

The distinguishing characters and habits of individual species of Myxomycetes during the entire vegetative period have rarely been reported in the literature. This is due principally to the fact that most of them vegetate within their substrata (Lister 1925), making it difficult to obtain their plasmodia for observation and study.

Hemitrichia vesparium (Batsch) Macbr. is such a species. It vegetates unseen within its substratum, where it also sclerotizes, and comes to the surface only to fruit. Although this species is commonly collected in the fruiting stage, there is no record in the literature to indicate that its true plasmodium has previously been recognized in the field.

The outstanding characteristic feature of the plasmodium is its stable, definitely black color. This color, unusual for slime-mold plasmodia, together with certain other constant features, makes specific identification possible before fruiting occurs. While taxonomic characters have not hitherto been reported for the vegetative stage of any species, it is believed, in view of the studies and observations made on this particular species, that they may be found to be rather widespread.

This report is based on observations made on forty-odd plasmodia of *H. vesparium* which were isolated and cultured during the past six years. These plasmodia and most of their subcultures fruited, bearing sporangia typical of the species. The sporangia were verified as to species by Mr. Robert Hagelstein, Honorary Curator of Myxomycetes at the New York Botanical Garden, who examined typical specimens of the sporangia submitted to him.

LITERATURE

The reports thus far published on *H. vesparium*, with one exception, are based on spore sowings made in the laboratory. They show that four-year-old spores have been found to be viable (Gilbert 1929); that the plasmodium is parasitic on fungus mycelia (Howard and Currie 1932); that the plasmodium requires no light in order to fruit (Gray 1938); and that the swarm-cells thrive well in pine wood decoction and can withstand temperatures as low at 2° C without encysting immediately (Smart 1938 a, b). Only two investigators have reported on the color of the plasmodium: Gray 1938, Carr 1939.

MATERIALS AND METHODS

The plasmodia of this species were obtained mostly by culturing decaying wood and leaves. Collections of such material were made in New York State (including Long Island, Gardiner's Island, and Staten Island), New Jersey, Pennsylvania, and southern Vermont. The plasmodium was isolated from material collected in all of these regions. Several plasmodia were grown from laboratory-developed fruiting bodies, the spores of which were sown on blotting paper which had previously been used as substratum. Numerous subcultures were also grown, some of them with other species in order to observe communal behavior. All of the plasmodia were cultured on white blotting paper, which was obtained in large desk-size sheets, watermarked in squares. The sheets were then cut to the desired size and shape as needed. Tap water was used as the source of moisture.

The method employed for isolating the plasmodia from their original substrata was to place a suitably sized disk of blotting paper, cut in halves, in a petri dish and moisten it with water. A selected piece of wood or leaves, recently collected and still moist, if possible, was then laid on the paper, and the culture kept saturated by subsequent additions of water as required. As soon as the plasmodium had left its original substratum, the latter was removed. Plasmodia thus isolated were given nutrient every few days, and were cultured and subcultured both in petri dishes and in jars.

When plasmodia were grown in jars, the method used was an adaptation of that employed by Camp (1936) in culturing *Physarum polycephalum*. Small glass-covered jars were preferred, which measured 3½ inches high and 2¾ inches in diameter. For starting these cultures, a portion of blotting paper containing the plasmodium was transferred from a petri dish culture to a jar that had been lined around the inside wall with two-inch squares of blotting paper and filled to a depth of about one inch with water. Such cultures provided the plasmodium with a continuous, partially submerged circuit or pathway around which it might travel progressively without inhibition, and also insured a constant supply of moisture.

Nutrient consisted of pulverized rolled oats (either the "Quick" or regular kinds), tropical fish food, and wheat germ. These were sifted on the cultures through a fine mesh sieve, in front of the plasmodial "fans." Fish food was used mostly for young plasmodia and for plasmodia which had become somewhat sluggish. It was also found to be good in preparing fresh blotting paper substrata. Usually, plasmodia would not creep onto a fresh piece of blotting paper sprinkled with oats until the second or third day, by which time the oats had become somewhat gelatinous. When fish food was used instead of oats, this time was generally reduced to a few hours. Oats, however, was decidedly the preferred nutrient, and was ingested readily later on as particulate food, after the plasmodium had become established

on a fresh piece of paper. Although no such definite reaction was noted in connection with wheat germ, it was continued in use in community cultures, along with oats, since plasmodia of some species thrive on it.

No effort was made to keep the cultures sterile, because it was felt that more natural results could be obtained if conditions approximated more closely those existing in nature. A given piece of blotting paper was therefore continued in use as substratum as long as it remained sufficiently firm, even though mold, bacteria, and other organisms were abundant in the culture. The surface was cleaned every week or ten days either by peeling off with tweezers the top layer of the paper or by flushing the culture with a siphoned stream of water, care being taken to avoid injuring the plasmodium.

CHARACTERS AND HABITS OF PLASMODIUM

The plasmodium is of medium size as compared with those of about fifty other species also grown in culture by the author. It is neither as large as *Physarum polycephalum* nor as small as several others cultured. This applies to the size of the largest veins as well as to the aggregate amount of protoplasm in a plasmodium which has attained its maximum growth.

As cultured, this species shows an ever changing "fan" pattern that is common among slime-molds, but the posterior veins are often looped (fig. 1). When young, it is frequently seen in a twin-fan pattern (fig. 2). The two fans are usually of equal size and are also connected posteriorly by looped plasmodial veins. This pattern may persist for as long as two days, when the fans may merge, or separate entirely. All of the twin-fan patterns observed were remarkably alike in form and size, and they were seen often enough to suggest the term "recurring pattern."

The plasmodial veins of this species vary greatly in diameter, although during the first few weeks they are usually of about equal size. Typical large veins consist of a main black-colored channel, flanked on either side by a thin, hyaline pseudopodial "ruffle" with darkened areas (fig. 3). These ruffles are always present throughout the life of the plasmodium, except when it is very young or very old. In a young plasmodium and in the smallest veins of an older one, the ruffles may be expressed merely as nodes or buds scattered along either side; in old plasmodia—those about ready to fruit—the ruffles have been withdrawn. The protoplasm is characterized by the presence of conspicuous, round, white transparent vacuoles, which are visible under a hand lens. They travel along with the protoplasm, which streams in one direction for about 50 seconds and then reverses its flow for about 45 seconds. The plasmodium, as a whole, advances at the rate of about an inch in three hours. These rates are about average for the slime-molds in general.

The black color of the plasmodium is derived from numerous black pigmented granules. These flow back and forth with the streaming protoplasm,

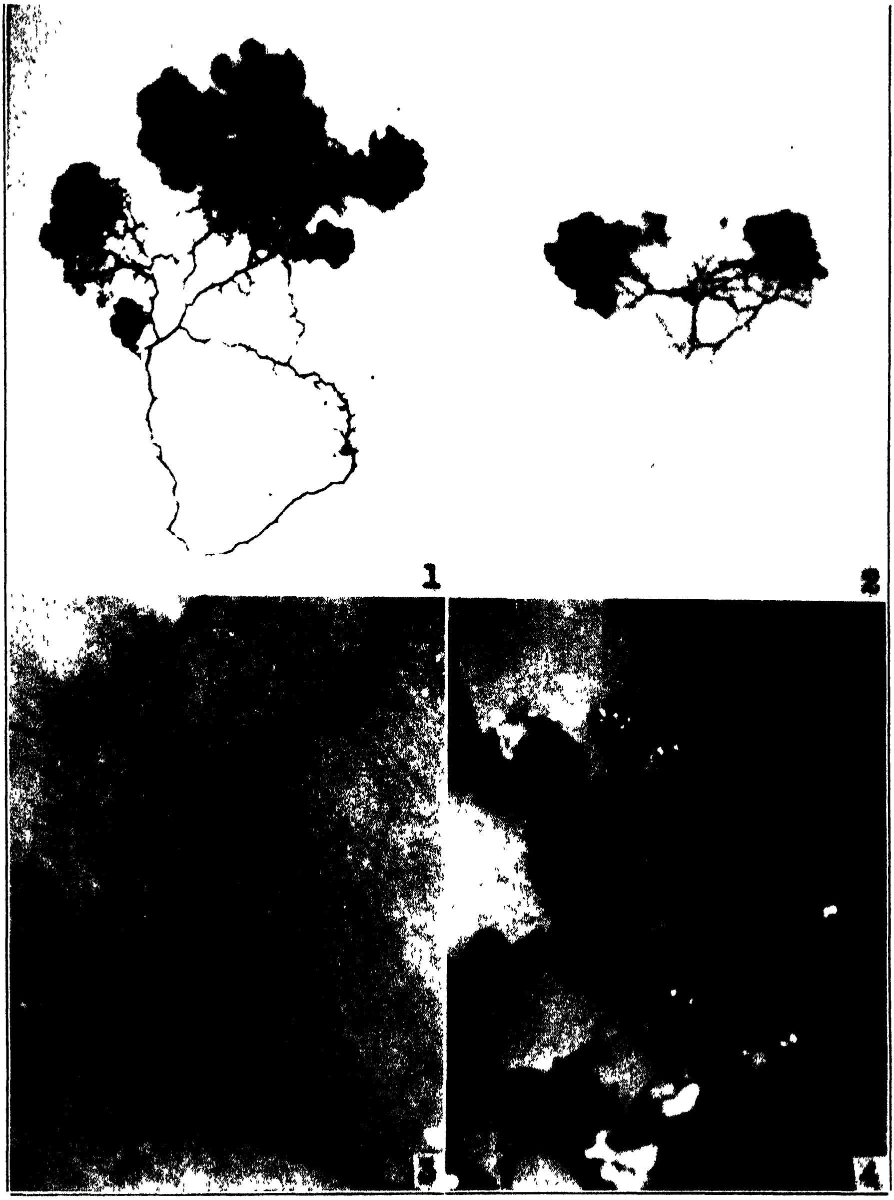


Fig. 1. Vegetating plasmodium, showing a normal variation in looping of posterior veins. ×3. Fig. 2. Recurring pattern. ×3. Fig. 3. Typical veins of a vegetating plasmodium, showing characteristic pseudopodial ruffles. ×30. Fig. 4. Plasmodial veins clumping to fruit. ×33.

being much more abundant in the main channels than in the hyaline pseudopodial ruffles. In these ruffles they are sparse at first, but wherever a number of them become temporarily lodged that area appears black (fig. 3). As the plasmodium ages, the granules seem to increase steadily in numbers throughout the entire plasmodium. As a result, there is a progressive deepening of the color during the vegetative stage. In this connection, Seifriz and Zetzmann (1935) reported that the deepening of the yellow color in the plasmodium of *Physarum polycephalum* is of the nature of a pH indicator, although they did not mention that the change in color was caused by the presence of pigmented granules.

In the field, the plasmodium is not found in places which would suggest that it requires an abundance of moisture; yet in culture it requires more than do plasmodia of those species most commonly grown in the laboratory, especially large ones such as *Physarum polycephalum* and *Fuligo septica.* This is particularly noticeable when the substratum begins to dry out. The two species just mentioned generally remain on the surface, while *H. vesparium* creeps into the substance of the paper and remains there until more moisture is provided. An exception to this habit occurs when the black plasmodium is nearing the fruiting stage, at which time it likewise remains on the surface. This abundance of moisture is evidently required to protect the hyaline pseudopodial ruffles against drying out, for the central vein channels were usually not covered by a film of water as were the ruffles. Keeping the cultures very wet also enabled the plasmodium to make more rapid growth. This species was never observed to creep up the bare sides of glass culture dishes as do the large yellow plasmodia of other species.

The vegetative stage of *H. vesparium* generally lasted from four to twelve months, seven being about the average. Plasmodia which were subcultured several times tended to take longer to fruit than did those not subcultured. One plasmodium grown from spores and not subcultured fruited in two months. Even this short period, however, was much longer than that recorded by Seifriz and Russell (1936) for *Physarum polycephalum,* which had a sixteen-day cycle in the cultures observed. Although no such specific periodicity was observed in *H. vesparium*, fructification was more certain to occur in this species than in any of the other species cultured.

Besides feeding on prepared nutrients, the plasmodium was also observed to ingest living organisms such as protozoa. Several times, when the plasmodium had crept off a small square of blotting paper in a petri dish into a thin film of surrounding water, various kinds of microscopic organisms swarmed and darted about the unusually long hyaline-tipped pseudopods that had just been elongated. After a few minutes a number of the organisms were engulfed by a quick outflow of more hyaloplasm. Several minutes later, black granular protoplasm was seen to stream out and carry the already disintegrating organisms deeper into the plasmodium.

Fragmentation was frequently observed in young plasmodia during the first two months; after that, it seldom occurred. The plasmodial fragments numbered anywhere from two to eight in a given culture at one time. In about a week they gradually coalesced into a single plasmodium, if permitted to, and then in another week or so fragmentation might recur.

In community cultures, the plasmodium was never observed to harm or interfere with a plasmodium of any other species with which it was associated. A small white plasmodium, however, was found to parasitize it (*H. vesparium*), completely consuming it. Over a three-year period, this parasitic plasmodium has been kept in the active vegetating state only by feeding it the plasmodium of *H. vesparium*, although many other nutrients were also tried. When it has no black plasmodium, it sclerotizes. Since parasitism among Myxomycetes themselves seems to be an unrecorded phenomenon, it seems better to prepare a separate illustrated report on the results obtained from culturing these two plasmodia together.

GROWTH OF PLASMODIUM AND SPORANGIAL FORMATION

During the plasmodial stage of *H. vesparium*, four periods of growth were observed: (1) when the plasmodium is very young (scattered nodes along equal-sized veins); (2) when older and making the most growth progress (main channels black, bordered by hyaline pseudopodial ruffles; veins varying in size); (3) when about mature (entire plasmodium, including ruffles, jet black; ruffles appear somewhat fringe-like); (4) when ready to fruit (ruffles entirely absent and main channels swollen and clumped). Although the appearance of the veins is not necessarily uniform throughout a given plasmodium at any one time, the characteristics of one of the four growth-periods enumerated always appear to predominate.

As the plasmodium approaches the fruiting stage, there is a sharp decrease in the amount of moisture and nutrient required. Only a moist substratum need now be maintained instead of a saturated one, and little if any nutrient is needed. Any nutrient that is inadvertently sifted directly upon a jet black plasmodium often causes that portion to turn red, such change of color denoting death in this species.

The amount of moisture present in a culture while the pseudopodial ruffles are disappearing seems to be the principal determinant of how soon afterwards the sporangia begin to rise. Excessive moisture tends to retard fructification and may even cause all or part of the plasmodium to die. Too little moisture inhibits its movement, and if the plasmodium is within the substratum at this time, it lies more or less dormant. Then when moisture is added, it has been observed to well up to the surface of its substratum, in shiny black masses, each a potential cluster of sporangia. At such times no hypothallus is seen, it being left behind within the substratum.

During the prefruiting period, the plasmodium may be either reticulate or in a solid layer. When in a layer, it resembles a thin sheet of shiny black wax in appearance. The veins of a reticulate plasmodium are greatly swollen at this time (fig. 4), and the protoplasmic streaming is very sluggish, as can be detected in the opaque veins only by means of the large transparent vacuoles. Close to a rising sporangial cluster, the streaming is in one direction only—toward and up into the sporangia, with no reversal flow taking place.

Sporangia require about four hours to complete development from the time they begin to rise from the clumped veins. The fruiting process generally occurs between midnight and morning, when no light is present. Although Gray (1938) did not mention this nocturnal habit for his plasmodia of this species, he did state that they required no light in order to fruit.

Fructification was never observed to occur as a result of injury to the plasmodium, lack of food, dehydration, or exposure to bright light. The plasmodia fruited, it seemed, only after a certain degree of maturity or aging had been attained. Camp (1937) reported that *Physarum polycephalum* could be induced to fruit at any time simply by withholding food from it. Such treatment of *H. vesparium* resulted only in a perceptible decrease in the size of its plasmodium. Seifriz and Russell (1936) stated that nutrition and toxic substances alone seemed to have a possible influence on the fruiting of *P. polycephalum*. They reported further that "the growth rhythm is believed to be a definite protoplasmic quality, which requires certain as yet unknown conditions in order to express itself."

Subcultures made from a parent plasmodium that was jet black and nearly ready to fruit, usually bore fruit about the same time as did the parent plasmodium. Seifriz and Russell (1936) also reported this fruiting habit for *P. polycephalum*.

All of the fruiting bodies which developed in culture were either one of the two colors reported by Gilbert (1927) for this species, namely, metallic bluish-black, or brick-red. The brick-red color predominated. Whether the amount of moisture in a culture had any relation to the color of sporangia produced was not determined, but at times this seemed probable.

FORMATION OF SCLEROTIA

The factors reported in the literature as causing Myxomycetes to sclerotize are: lack of food, dehydration, and cold. The last two were the only ones observed to cause the plasmodium of *H. vesparium* to sclerotize. Lack of food, as has just been mentioned, only resulted in a decrease in the size of the plasmodium.

In most instances, sclerotia of this species formed as a result of dehydration. Unlike many larger species, which sclerotize in a heaped mass on the

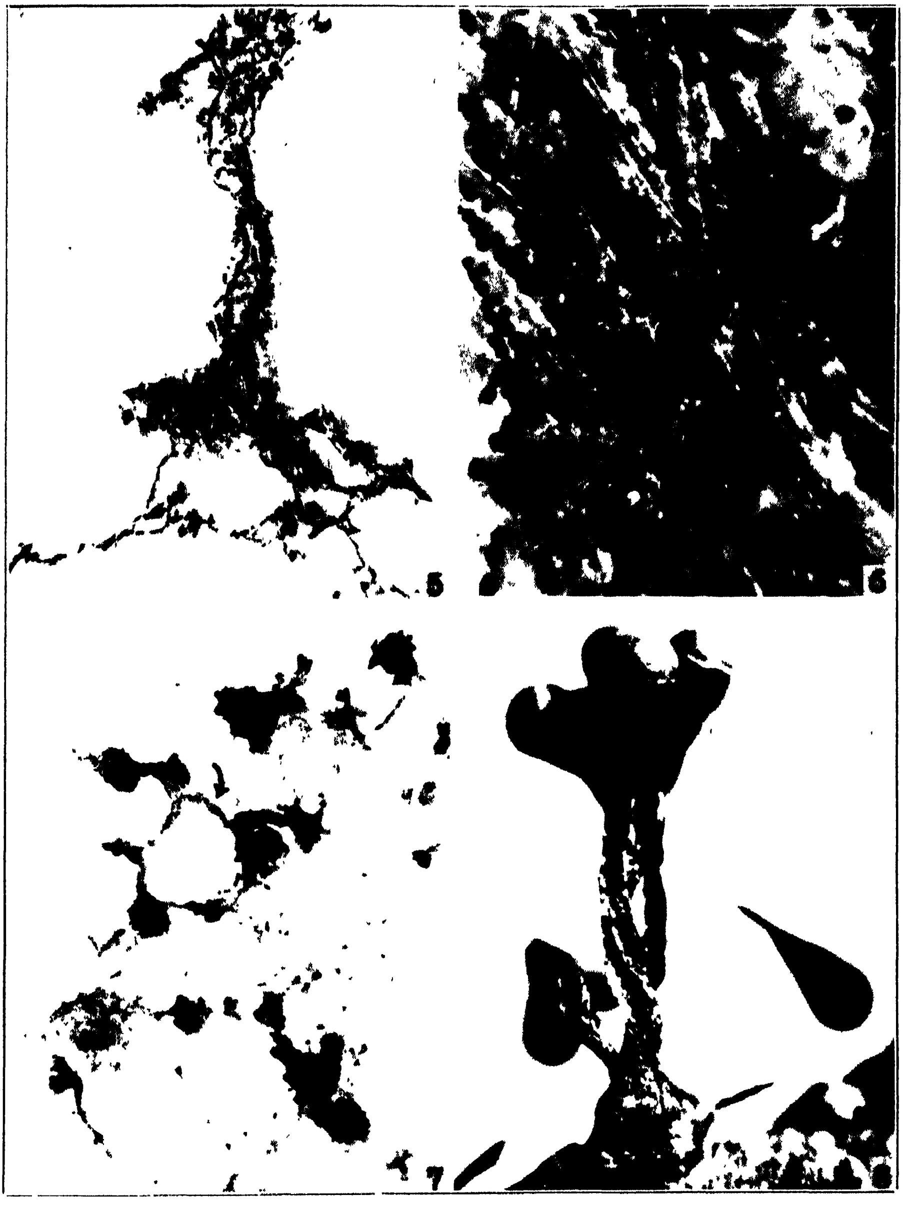


FIG. 5. A sclerotized plasmodium between blotting paper and glass. × 33. FIG. 6. Middle section of figure 5 enlarged. × 150. FIG. 7. Portion of a culture that has fruited, showing dorsal view of sporangial clusters and the red residue left in former vein tracks when the plasmodium fruited. × 3. FIG. 8. Typical sporangia. × 30.

surface of their substratum when dehydration occurs, *H. vesparium* sclerotizes within its substratum (or beneath it) in rows of black bead-like cysts (figs. 5 and 6). This formation results from the breaking up of the plasmodial veins *in situ*.

The cysts are generally round or ovoid in shape when fresh, and range in size from 10 to 40 μ. If formed within blotting paper, a large sclerotium resembles a light-colored blot of ink when viewed from either side without a lens, the individual cysts not being visible. A small sclerotium can sometimes be located only by holding the paper up to the light. When the sclerotium forms beneath the blotting paper, next to the glass, the rows of cysts show up plainly under low magnification. Young cysts that were formed as a result of dehydration required only a day or two to excyst after being moistened, while one-year-old cysts required from 48 to 60 hours.

Exposure to cold caused the plasmodium to sclerotize even when it was covered with water. When subjected suddenly to a temperature of 40° F., the plasmodium sclerotized in about 12 hours. This change occurred so quickly that the original pattern of the plasmodium was retained and a low magnification was required to show that encystment had taken place. Some of the cysts became a transparent red in color and could not be revived, but those that remained black usually could be reactivated into normal plasmodia within a day or so.

Plasmodia that developed from reactivated sclerotial cysts were always black and bore typical sporangia (fig. 8).

PLASMODIAL COLOR

Although black was the only color observed either in the field or in the laboratory for *H. vesparium*, this color does not seem to be mentioned in the literature for this species or for any other vegetating Myxomycete, and inquiry among students of these organisms revealed no one who had previously seen a black plasmodium. In a few instances taxonomists have listed some shade of black as the plasmodial color of a few species, but such color references apparently are not meant to apply to the vegetative stage—as is generally interpreted—but to the prefruiting stage (that which immediately precedes fructification). Macbride (1922, p. 286) states that the colors listed in *The North American Slime-Moulds* refer to the prefruiting stage unless otherwise stated. Hagelstein makes a similar statement regarding colors of vegetating plasmodia, in a personal communication (1938). Since Macbride lists the color of *H. vesparium* as deep red (l. c., p. 262) and does not specify the stage to which it belongs, he, and others who also list some shade of red for the plasmodial color of this species, must therefore mean the color red to refer to the prefruiting stage, and not to the vegetative stage as was concluded by Gray (1938) and Carr (1939).

Gray reported that his plasmodia of this species, which he obtained by sowing spores on corn agar, were pearly white. He stated, however, that they did not grow large, that fruiting was sporadic, and that in no case was an entire plasmodium utilized in sporangial formation. A few of the black plasmodia that I have grown from spores on blotting paper and not transferred or subcultured had a tendency to be somewhat erratic in their fruiting habit in that the plasmodial fragments sometimes remained separate and fruited at different times. In each instance observed, however, all of the protoplasm in a given plasmodial unit was utilized when fructification occurred. This was generally true, also, of plasmodia obtained from material in the field, which, like those grown from spores, sometimes formed five-inch fans when given sufficient space and fed carefully.

It may be pointed out, in connection with Gray's reporting a different color for the vegetative stage of this species, that according to the literature the use of prepared media in culturing spores of Myxomycetes has not proved to be a very reliable source from which to determine colors of vegetating slime-mold plasmodia. Pinoy (1908) reported that he obtained yellow plasmodia as well as blackish-purple ones when he sowed spores of *Didymium nigripes* on flaxseed gelatin. Gray (1938) and Kambly (1939) obtained yellow and white plasmodia, respectively, by sowing spores of *Fuligo septica* on corn agar. On the other hand, plasmodia of *H. vesparium*, according to my observations, were always black, whether observed in the field, isolated from natural substrata on blotting paper, or grown from spores on blotting paper.

Still another color has been reported for this species. Carr (1939), after observing a single plasmodium on wood cultured in a moist chamber for four months and then finding fruiting bodies of *H. vesparium* on the wood, concluded that the yellow plasmodium had borne the sporangia of this species. The evidence is inconclusive. Many times the author has also had sporangia of this species develop on decaying wood cultured in a moist chamber, when the only visible plasmodium was a yellow one. But when such pieces of wood were cultured with a view to isolating all Myxomycete plasmodia present in the wood, as many as four or five other plasmodia, all differently colored, were frequently obtained; that of *H. vesparium* (always black) was often one of them and the only one that produced typical fruitings of this species when grown in isolated cultures. It is therefore doubtful that *H. vesparium* ever has a yellow plasmodium.

Regarding the red color listed by Macbride and other taxonomists as the prefruiting color of *H. vesparium*, this color was not observed in any of the black plasmodia preceding nor during their fruiting period. Sometimes, when viewed by reflected light, the plasmodium had a faint red tinge shortly before fruiting time. This was thought to be due to the presence of extraneous material that was beginning to be cast off, for as the jet black protoplasm

flows into the newly forming fruiting bodies, it leaves a red residue behind in the vein tracks (fig. 7, *arrow*). When fresh, this red residue so closely resembles living plasmodium in consistency that microscopical examination under good light was necessary in order to determine its true nature. Because of this close resemblance, it is wondered whether the appearance of this red residue at fruiting time might account for the statements of Macbride and others that the prefruiting color was red. It would undoubtedly show up more clearly than would black on dark, decaying vegetation. It might even account for Gray's observing (1938) that his pearly white plasmodia of this species turned red at fruiting time but that this color change did not occur until after sporangial delimitation had begun. To determine this point, further observation seems necessary.

Although color as a taxonomic character of vegetating slime mold plasmodia has not yet been recognized, it may not be without significance in helping to determine species of Myxomycetes before fruiting occurs. The consistency with which *H. vesparium* has maintained its color over such a long period of time affords evidence in this direction. Kambly (1939) believes that it is necessary to know the factors influencing color before it can be accepted as a taxonomic character. When color has been found to be constant for a given species, however, it seems logical to recognize its taxonomic value without waiting to determine what causes it.

31 Pondfield Road West
Bronxville, New York

SUMMARY

1. The plasmodium of *H. vesparium* can be identified specifically before fruiting occurs and is easily cultured to maturity. It is characterized by a definite black color.

2. Fragmentation occurs frequently during the early life of the plasmodium.

3. The plasmodium has a recurring twin-fan pattern. Posterior veins are often looped.

4. Sclerotia are formed within the substratum in rows of bead-like cysts.

5. The plasmodium is completely parasitized in culture by the plasmodium of another Myxomycete (species as yet undetermined).

Literature Cited

Camp, W. G. 1936. A method of cultivating Myxomycete plasmodia. Bull. Torrey Club **63:** 205–210.

————. 1937. The fruiting of *Physarum polycephalum* in relation to nutrition. Am. Jour. Bot. **24:** 300–303.

Carr, Lloyd G. 1939. The plasmodium of *Hemitrichia Vesparium* (Batsch) Macbr. Science **90:** 329.

Gilbert, Frank A. 1927. Notes on Myxomycetes from eastern Massachusetts. Rhodora **29:** 165–173.

————. 1929. Spore germination in the Myxomycetes: A comparative study of spore germination by families. Am. Jour. Bot. **16:** 421–432.

Gray, William D. 1938. The effect of light on the fruiting of Myxomycetes. Am. Jour. Bot. **25:** 511–522.

Howard, Frank L. & Currie, Mary E. 1932. Parasitism of Myxomycete plasmodia on fungous mycelia. Jour. Arnold Arb. **13:** 438–447.

Kambly, Paul E. 1939. The color of Myxomycete plasmodia. Am. Jour. Bot. **26:** 386–390.

Lister, G. 1925. Mycetozoa. London.

Macbride, Thomas Huston. 1922. The North American Slime Moulds. New York.

Pinoy, E. 1908. Sur l'existence d'un dimorphisme sexuel chez un Myxomycete, *Didymium nigripes*. Compt. Rend. Soc. Biol. **64:** 630–631.

Seifriz, William & Russell, Mary A. 1936. The fruiting of Myxomycetes. New Phytol. **35:** 472–478.

Seifriz, William & Zetzmann, M. 1935. A slime mould pigment as indicator of acidity. Protoplasma **23:** 175–179.

Smart, Robert F. 1938a. The reactions of Myxomycetous swarm-cells to temperature. Am. Jour. Bot. **25:** 679–682.

————. 1938b. The reactions of the swarm cells of Myxomycetes to nutrient materials. Mycologia **30:** 254–264.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 164–173 MARCH, 1943

MACROSPOROGENESIS, FERTILIZATION, AND EARLY EMBRYOLOGY OF TARAXACUM KOK-SAGHYZ[1]

H. E. WARMKE

With the introduction of seed of the Russian Dandelion, *Taraxacum kok-saghyz* Rod., into this country early in 1942, and with plans for its extensive cultivation as a domestic source of rubber, it became important to know something more of the cytology and breeding behavior of this species.

The common dandelion, *Taraxacum officinale,* and other species have long been known to reproduce by apomixis (Raunkiaer 1903; Murbeck 1904; Juel 1904, 1905; Sears 1917, 1922). In these forms there is a failure of the first meiotic division, and the second division gives rise to a dyad of macrospores with unreduced nuclei, rather than the usual tetrad with reduced chromosome number (Osawa 1913; Rosenberg 1927, 1930). One of the unreduced cells degenerates (usually the micropylar one), and the other undergoes mitotic divisions to form an eight-nucleate, but diploid, embryo sac. The unreduced egg cell begins to divide, without the stimulation of fertilization, to form a completely vegetative embryo and seed.

With apomixis known to occur in the genus, it was important to ascertain whether the material with which we were working was also apomictic, or whether it was sexual, before entering into selection and breeding experiments. The Russian workers, Poddubnaja-Arnoldi and Dianowa (1934), in a study of several members of the genus, reported *T. kok-saghyz* to be a diploid with chromosome numbers of $n = 8$; $2n = 16$. They further reported that this species is sexually reproducing and highly self-sterile. Our results confirm and extend the findings of these workers.

MATERIALS AND METHODS

Seeds were received on May 16, 1942, from Dr. E. W. Brandes under the label, *Taraxacum kok-saghyz,* plant quarantine number 143960. These were a portion of the seeds which reached this country from Russia by air express. They apparently were from unselected field-grown plants, for in addition to showing extreme variation in size, vigor, and leaf shape, they also contained contaminations of the common dandelion.

Root tips were prepared according to the section-smear technique (Warmke 1941). Buds and flowers were fixed in Rollin Carnoy, sectioned at 10–20 microns according to the stage, and stained with the Feulgen reaction for fertilization and iron hematoxylin for other stages.

[1] Cooperative project with Dr. E. W. Brandes, Pathologist in Charge, Rubber Plant Investigations, U. S. Department of Agriculture.

CHROMOSOME NUMBER

Root tips were taken from plants growing in four-inch pots in the greenhouse; chromosome counts showed the diploid number to be 16 (fig. 1, a and b). No variation from this number has been observed. The chromosomes are of medium size, ranging from approximately 2 to 4 microns in length in the roots, and fix and stain well. One pair of chromosomes bears prominent satellites (fig. 1, b).

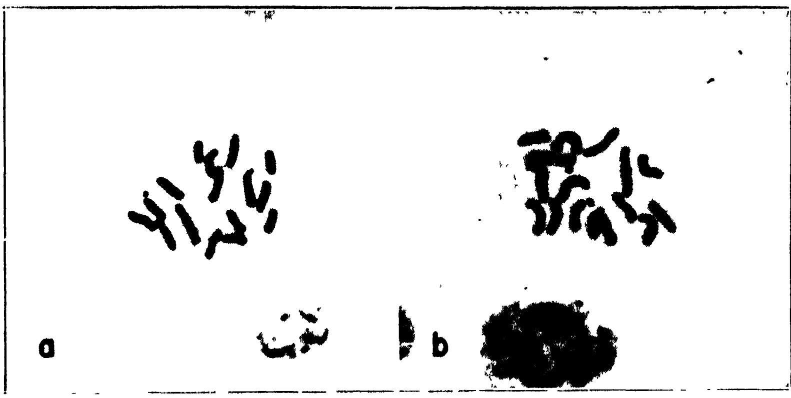


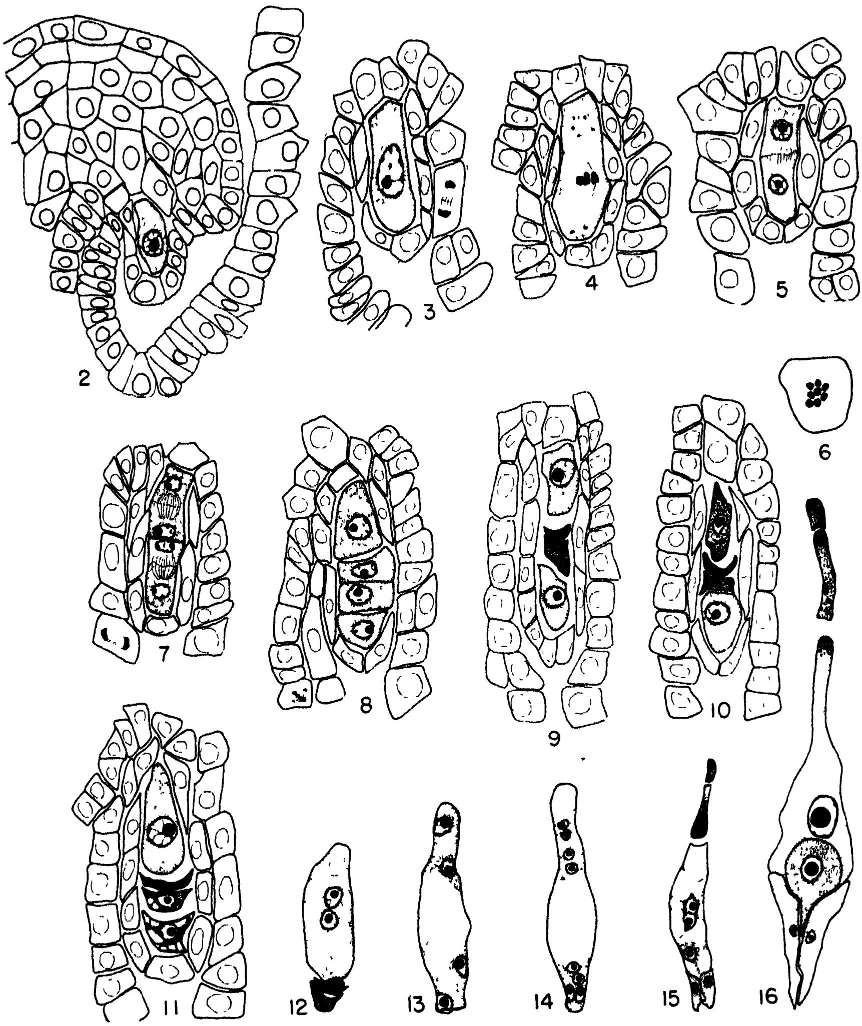
FIG. 1. Photomicrographs of somatic chromosomes from root tips of *Taraxacum kok-saghyz*. The diploid chromosome number is 16. Note one pair of chromosomes with satellites (fig. 1b). × 1400.

The haploid chromosome complement was studied at first meiotic metaphase in macrospore mother cells (fig. 4) and in pollen mother cells (fig. 6). In all cases the reduced chromosome number was found to be 8.

DEVELOPMENT OF THE MACROGAMETOPHYTE

The ovule is solitary and anatropous. The macrospore mother cell arises from a hypodermal cell and may be distinguished early by its greater size and more intense staining reaction (fig. 2). Surrounding the macrospore mother cell is a single layer of nucellar cells, which is soon overgrown and surrounded, except for the micropyle, by a single integument. The macrospore mother cell increases further in size (fig. 3) and then undergoes the first meiotic division (fig. 4). The chromosomes are arranged in a regular manner as bivalents on the metaphase plate, with no indication of univalents or laggards.

At the end of MI a cell wall is laid down (fig. 5) to form the usual dyad. The second meiotic division follows quickly, and cell walls are laid down to form a linear tetrad of macrospores (figs. 7, 8). The chalazal macrospore tends to be larger than the others (fig. 8) and usually becomes functional,



FIGS. 2–16. Meiosis and macrogametophyte formation in *T. kok-saghyz*. FIG. 2. Young ovule showing macrospore mother cell before overgrowth of the integument. × 540. FIG. 3. Older macrospore mother cell. × 540. FIG. 4. First meiotic metaphase; eight bivalent chromosomes are present. × 540. FIG. 5. Late telophase of first meiotic division with dyad of cells being formed. × 540. FIG. 6. MI in pollen mother cell showing 8 chromosomes. × 840. FIG. 7. Late telophase of second meiotic division. × 540. FIG. 8. Linear tetrad of macrospores. × 540. FIG. 9. Middle two spores of tetrad tend to degenerate early. × 540. FIG. 10. A rare case, where micropylar macrospore is functional. × 540. FIG. 11. The more usual condition, where the chalazal macrospore becomes functional, and the others degenerate. × 540. FIGS. 12–14. 2-, 4-, and 8-nucleate stages in the development of the macrogametophyte. × 270. FIG. 15. Young 7-celled macrogametopyte. Note union of the polar nuclei and beginning of degeneration of antipodals. × 270. FIG. 16. Mature macrogametophyte. × 270.

while the three other macrospores degenerate (fig. 11). There is a strong tendency in many of the ovules, however, for the middle two cells to degenerate quickly and for both the micropylar and chalazal ones to persist and enlarge (fig. 9). One of these eventually gains the ascendency and the other degenerates, for twin embryo sacs have not been observed. The basal cell usually becomes functional, but figure 10 shows a case where the micropylar cell seems to have become the functional macrospore.

This process appears to be an orderly and complete meiotic division and to have resulted in the formation of four reduced macrospores. It is quite distinct from the abortive process in the common apomictic species, in which two unreduced macrospores are formed as the end-result of meiosis.

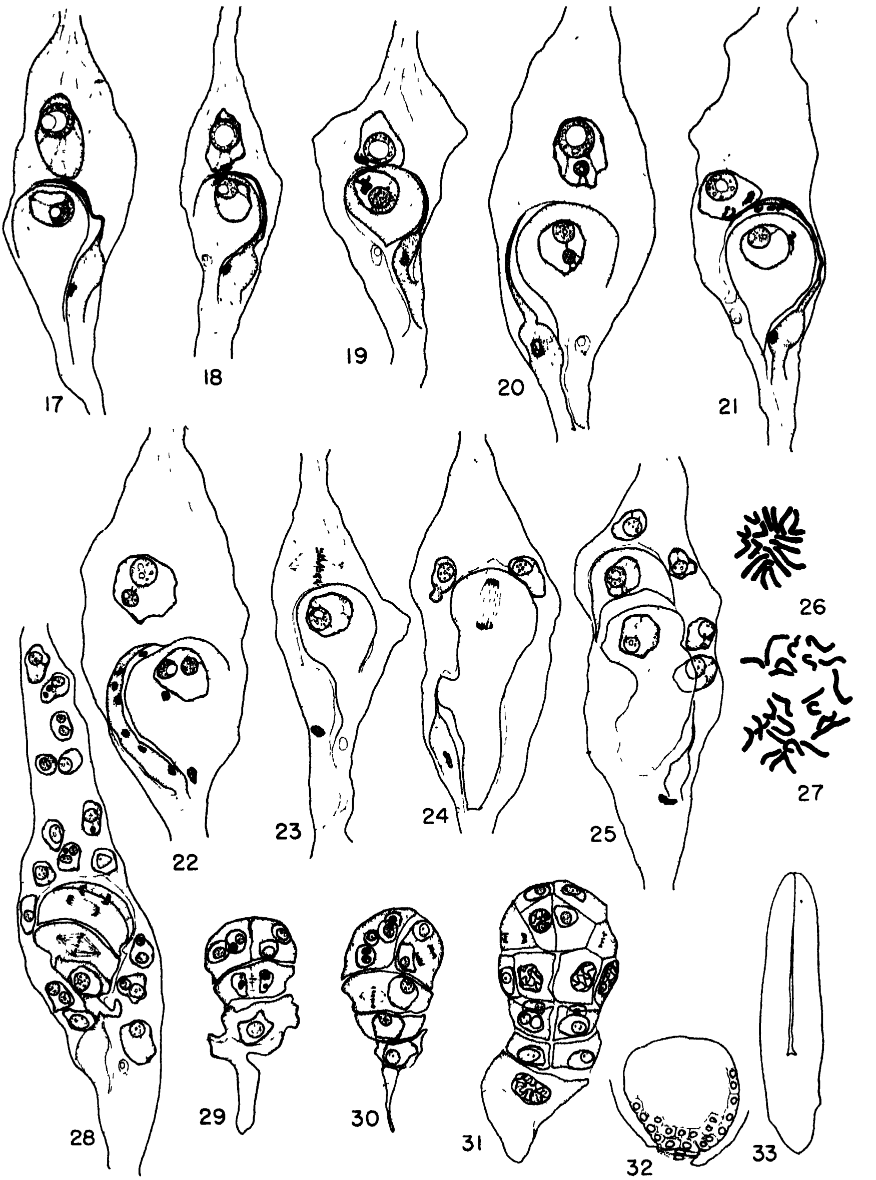
Before the non-functional spores have completely degenerated, the first mitotic division in the formation of the macrogametophyte occurs (fig. 12). The second and third divisions follow in rapid succession, forming four-nucleate (fig. 13) and eight-nucleate (fig. 14) macrogametophytes. During these free nuclear divisions the macrogametophyte increases in size, largely by the process of vacuolation. It is also evident that as the number of nuclei increases, the individual nuclei decrease in size (figs. 12–14).

The two most centrally located nuclei approach each other in the usual manner to become the polar nuclei (fig. 15). Note in figure 15 that these two nuclei, though in contact, are still separated by the nuclear membranes. Cell walls are laid down and soon transform the macrogametophyte into the typical seven-celled structure, consisting of two synergids, an egg cell, a large and vacuolate primary endosperm cell, and three antipodals. These latter become pycnotic and start to degenerate even before the polar nuclei have completely fused (fig. 15). The macrogametophyte enlarges greatly until it reaches its mature size (fig. 16), which represents the condition at flowering.

FERTILIZATION

Fertilization begins about 30 minutes after pollination at 70° F. under greenhouse conditions. This may be compared with 15 minutes reported for this species under slightly different conditions by Poddubnaja-Arnoldi and Dianowa (1934). Our fixations at 10, 15, 20, and 25 minutes failed to show evidence of fertilization.

Thirty minutes after pollination many ovules are seen in which pollen tubes have penetrated the embryo sac (apparently through a synergid) and have wedged in between the egg and primary endosperm cells, separating these structures (fig. 17). Whether this is actually the tip of the pollen tube, or some material extruded from the tube, is not clear. This material is uniform in consistency and appears to be somewhat more dense than the cytoplasm of the surrounding embryo sac. It has a characteristic sickle shape and bears near its base a single small nucleus which stains darkly. It is not cer-



FIGS. 17–33. Fertilization and embryo formation in *T. kok-saghyz*. FIG. 17. 30 minutes after pollination: pollen tube with two male nuclei near its tip within the embryo sac. ×380. FIG. 18. 30 minutes after pollination: male nuclei in contact with nuclear membranes of egg and endosperm cells. ×380. FIG. 19. 45 minutes after pollination: male nuclei within egg and endosperm nuclei. ×380. FIG. 20. 2 hours after pollination: the intensely staining male nuclei have disappeared and are replaced by small extra nucleoli within egg and endosperm nuclei. ×380. FIGS. 21, 22. 45 minutes and 2 hours,

tain whether this is the tube nucleus or the nucleus of the synergid which was penetrated by the pollen tube, although the latter seems more likely, since this pycnotic nucleus always lies approximately opposite the undisturbed synergid nucleus (figs. 18, 19, 20, 21).

With the Feulgen reaction, the large egg and endosperm nuclei take a very light stain, in contrast to the sperm nuclei, which stain very intensely. When first seen, the male nuclei appear to lie within the pollen-tube material (fig. 17) but soon come to lie out of this and in contact with the egg and endosperm nuclei (fig. 18).

Forty-five minutes after pollination the two male nuclei are seen inside the egg and endosperm nuclei; they have increased in size, and have become more diffuse (fig. 19). In favorable preparations male nuclei at this stage are seen to be made up of expanding and uncoiling chromonemata. At two hours, nuclear fusion is complete (fig. 20). The intensely staining chromatin of the male nuclei is no longer in evidence; in its place two small nucleoli have appeared, one each in the egg and endosperm nuclei. The pollen-tube material is still present, as well as the cavity separating egg and endosperm cells.

As noted by the Russian workers, supernumerary male nuclei are not uncommon. Figures 21 and 22 show two such cases. In the first of these a total of 8 male nuclei is present in one embryo sac; while the second must have 10: 8 densely staining ones and two already united with the egg and endosperm nuclei, as indicated by the presence of two nucleoli in each of these nuclei. Figure 22 is a two-hour stage, and the double nucleoli almost certainly indicate previous nuclear fusion, just as they do in figure 20.

The supernumerary sperm nuclei usually do not function, as is indicated by their presence as separate, compact bodies lying in the pollen-tube material or adjacent cavity even after the egg and endosperm have begun mitotic divisions. Figure 21, however, seems exceptional: here two nuclei lie in the tube, three in the adjacent cavity, one against the egg nucleus, and two against the primary endosperm nucleus. The sperm nuclei in contact with the egg and the endosperm nuclei are becoming diffuse. This suggests

respectively, after pollination: supernumerary male nuclei are occasionally found within the embryo sac. ×380. FIG. 23. 6 hours after pollination: the endosperm nucleus is undergoing its first division. ×380. FIG. 24. 7 hours after pollination: the endosperm is 2-nucleate, and the zygote is undergoing the first division. ×380. FIG. 25. 9-hour stage: the proembryo is 2 celled, and the endosperm is 4 nucleate. ×380. FIG. 26. Metaphase plate from dividing embryo cell showing diploid number of chromosomes, $2n = 16$. ×1400. FIG. 27. Late prophase from dividing endosperm showing triploid number of chromosomes, $3n = 24$. ×1400. FIG. 28. Proembryo 4-celled, and endosperm 16-nucleate. ×380. FIG. 29. 7-celled proembryo. ×380. FIG. 30. 11 celled proembryo. ×380. FIG. 31. 24 hours after pollination: proembryo is made up of 28–30 cells. ×380. FIG. 32. 40–44 hours: young spherical embryo with short suspensor. ×85. FIG. 33. 55–60 hours: the embryo has assumed mature form, with cotyledons, epicotyl, hypocotyl, and root tip. ×25.

that these two male nuclei, instead of one as expected, may be uniting with the endosperm. There is some further evidence that functional polyspermy may occur in connection with the endosperm, in the fact that four or five separate nucleoli may occasionally be observed in a single endosperm nucleus. Since a maximum of one nucleolus is characteristic of each haploid chromosome complement, the presence of four or five nucleoli in endosperm cells may be indicative of extra sets of chromosomes, although no more than the triploid number of chromosomes has ever actually been counted in dividing endosperm.

DEVELOPMENT OF THE EMBRYO AND ENDOSPERM

At approximately 6 hours after pollination, under our conditions, the first division of the endosperm occurs (fig. 23). This is usually followed about an hour later by the division of the zygote (fig. 24). At 9 hours after pollination the proembryo is 2-celled and the endosperm 4-nucleate (fig. 25). Chromosome counts from dividing cells show the embryo to be diploid (fig. 26) and the endosperm to be triploid (fig. 27).

The further development of the embryo follows the "aster type," characteristic of the composites. The "basal cell" (according to the terminology of Souèges) undergoes a transverse division; while the "apical cell" divides in a longitudinal plane. This is illustrated in the 4-celled stage (fig. 28). Here the basal cell has divided to form two daughter cells, one above the other; while the apical cell has divided so that one daughter cell lies behind the other.

The second division of the apical cell is also longitudinal, but at right angles to the plane of the first, as shown by the orientation of the division figures in figure 28. The uppermost half of the original basal cell also divides longitudinally, thus producing a 7-celled proembryo (fig. 29).

The proembryo undergoes rapid division to reach the 11-celled stage shown in figure 30. There are 7 derivatives of the original apical cell and 4 derivatives of the original basal cell. At 24 hours the proembryo has a total of 28–30 cells (fig. 31).

At 40–44 hours the embryo proper has formed a flat ball of several hundred cells, with a short suspensor consisting of 8–12 cells (fig. 32). At about 60 hours the embryo has attained mature appearance with well developed cotyledons, epicotyl, hypocotyl, and root tip (fig. 33).

BREEDING BEHAVIOR

The first flowers were observed August 16 on greenhouse-grown plants; this was exactly three months after sowing the seed. Plants have continued to come into flower throughout the fall and winter, with approximately one-third having flowered by January 1, 1943. During the summer and early fall

none of the plants that flowered set any seed, unless they were mechanically cross-pollinated by rubbing together heads from different plants. After such cross-pollination abundant seed was set, which ripened in about 10 days. The greenhouses were screened against insects; so this behavior indicates a high degree of self-sterility. Even when plants were mechanically self-pollinated by rubbing two flowers from the same plant together, seeds failed to set. Plants of the common apomictic species of dandelion, of course, set seed abundantly without any sort of pollination under identical conditions.

During November and December, however, many *T. kok-saghyz* plants began to set seed without cross-pollination. Some of these heads bore only 1 or 2 seeds while others bore a full set of 50–75 seeds. It would appear that this is an "end-season fertility," induced possibly by temperature, light, or age of the plant. It has not yet been possible, however, to show definitely that this delayed fertility is due to selfing and not to apomixis; but it seems highly improbable that the latter could be the case.

DISCUSSION

Chromosome numbers of $n=8$ and $2n=16$ place *T. kok-saghyz*, along with six or eight other species, as basic diploids in the genus. The great majority of the genus, however, is polyploid. Species with sporophytic chromosome numbers of 24, 32, and 40, representing triploid, tetraploid, and pentaploid forms, respectively, are known. It is of interest that the diploid species, including *kok-saghyz*, are sexually reproducing, while the polyploids are apomictic. This close correlation between polyploidy and apomixis has long been noted but is not yet thoroughly understood. As pointed out by Stebbins (1941) hybridization and polyploidy may be factors in bringing together complementary genes for apomixis and in the production of vigorous sterile or partially sterile types in which apomixis would have a very high selective value.

The reproductive process in *T. kok-saghyz* is completely normal and sexual. On the female side, where sexual reproduction breaks down in apomictic species, two regular meiotic divisions occur to produce a linear tetrad of reduced macrospores. There can be no doubt about the occurrence of fertilization: all stages, from the entrance of the pollen tube to complete union of the male nuclei with egg and endosperm, have been observed. Moreover, when pollination and fertilization do not occur, there is no development of embryo or endosperm. Final proof of the reality of the reduction divisions and of fertilization is afforded by actual chromosome counts, in which the developing embryo has been shown to be diploid (16 chromosomes) and the developing endosperm triploid (24 chromosomes). Presumably the embryo would be diploid and the endosperm tetraploid if this species were apomictic.

These conditions, including ample heterozygosity, low chromosome num-

ber, normal sexual reproduction, and a high degree of self-sterility, are extremely favorable from the standpoint of breeding and selection experiments. With satisfactory methods of assaying the rubber content of individual plants, the breeding of these plants and the selection of strains with improved cultural and rubber-producing qualities should be routine for the experienced plant breeder.

SUMMARY

1. The chromosome number in *Taraxacum kok-saghyz* is $n = 8$; $2n = 16$, placing this species among the basic diploids of the genus.

2. Macrogametophyte formation follows the usual sexual pattern: The macrospore mother cell undergoes two regular meiotic divisions to form a linear series of four reduced macrospores, the chalazal one of which usually becomes functional. As the result of three successive mitotic divisions followed by union of the two polar nuclei and cell wall formation, the classic 7-celled macrogametophyte is formed.

3. Thirty minutes after pollination, pollen-tubes are seen to enter the macrogametophyte. Fertilization follows the normal pattern: one male nucleus uniting with the egg and the other uniting with the primary endosperm nucleus. Supernumerary male nuclei are frequently observed in the embryo sac but usually are not functional.

4. The first division in the endosperm occurs about 6 hours after pollination, and the first division of the egg follows about one hour later.

5. Embryonic development follows the aster type, characteristic of the compositae.

6. Chromosome counts verify the reality of the sexual processes by showing the developing embryo to be diploid, with 16 chromosomes, and the endosperm to be triploid, with 24 chromosomes.

7. During the summer *T. kok-saghyz* is highly self-sterile but cross-fertile. In the late fall and winter it may exhibit considerable end-season self-fertility.

DEPARTMENT OF GENETICS, CARNEGIE INSTITUTION OF WASHINGTON
COLD SPRING HARBOR, NEW YORK

Literature Cited

Juel, H. O. 1904. Die Tetradenteilungen in der Samenanlage von *Taraxacum*. Ark. Bot. **2**: 1–9.

———. 1905. Die Tetradenteilung bei *Taraxacum* und anderen Chichorieen. Svensk. Vet.-Akad. Handl. **39**: 1–21.

Murbeck, Sv. 1904. Parthenogenese bei den Gattungen *Taraxacum* und *Hieracium*. Bot. Not. **1904**: 285–296.

Osawa, J. 1913. Studies on the cytology of some species of *Taraxacum*. Arch. Zellforsch. **10**: 450–469.

Poddubnaja-Arnoldi, V. & Dianowa, V. 1934. Eine zytoembryologische Untersuchung einiger Arten der Gattung *Taraxacum*. Planta **23:** 19–46.

Raunkiaer, C. 1903. Kimdannelse uden Befrugtning hos Maelkebøtte (*Taraxacum*). Bot. Tidssk. **25:** 109–139.

Rosenberg, O. 1927. Die semiheterotypische Teilung und ihre Bedeutung für die Entstehung verdoppelter Chromosomenzahlen. Hereditas **8:** 305–338.

————. 1930. Apogamie und Parthenogenesis bei Pflanzen. Handb. Vererb. II. 1–66.

Sears, P. B. 1917. Amiotic parthenogenesis in *Taraxacum vulgare* (Lam.) Schrk. and *Taraxacum laevigatum* (Willd.) Dc. Ohio Jour. Sci. **17:** 97–100.

————. 1922. Variations in cytology and gross morphology of *Taraxacum*. I. Cytology of *Taraxacum laevigatum*. Bot. Gaz. **73:** 308–325.

Stebbins, G. L. 1941. Apomixis in the Angiosperms. Bot. Rev. **7:** 507–542.

Warmke, H. E. 1941. A section smear method for plant cytology. Stain Tech. **16:** 9–12.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 2, p. 174 MARCH, 1943

TWO NEW SPECIES OF HYPERICUM FROM COLOMBIA

H. A. GLEASON AND J. H. PIERCE

In recent Cuatrecasas collections from northeastern Colombia the following two new species of *Hypericum* were found. They belong to the section *Brathys*, subsection *Eubrathys*, which has been previously treated by Gleason.[1]

Hypericum garciae Pierce sp. nov. Frutex ramis virgatis vel erectis inferne denudatis; folia rigida laxe imbricata, anguste lanceolata, 6–7 mm. longa, 1.3 mm. lata, punctata, margine integerrimo revoluto, nervo medio subtus prominenti, nervis lateralibus nullis; flores solitarii ad apices ramulorum; sepala ovato-lanceolata, 5.8–6.2 mm. longa, 1.5–1.8 mm. lata; petala oblique obovata, apiculata, 10 mm. longa; ovarium ovatum, uniloculare, 3–4 mm. longum, septis nullis, placentis 3 parietalibus; styli 3, 5.5–5.8 mm. longi.

TYPE, *Cuatrecasas* & *Garcia Barriga 9935*, collected on the Paramo del Almorzadero, Dept. of Santander, in the Cordillera Oriental of Colombia, and deposited in the Britton Herbarium of the New York Botanical Garden. This species resembles closely *H. chamaemyrtus* Tr. & Pl. but differs in having smaller, more strictly ascending leaves, solitary flowers, smaller petals, fewer stamens, shorter styles, and a larger ovary.

Hypericum cuatrecasii Gleason sp. nov. Frutex ramosus ramis inferne denudatis bialatis infra foliorum costam mediam. Laminae subcoriaceae patulae late rotundo-ovatae, usque 7 mm. longae lataeque, aut in ramulis tantum 2 mm. longae, ad basim cordato-amplectentes paulo connatae, 1-nerviae, venulis, reticulatis vix perspicuis. Pedicelli brevissimi, calyce foliis superioribus fere obtecto. Sepala ovato-elliptica obtusa, 5–5.3 mm. longa, 3–3.9 mm. lata. Petala asymmetrica 12 mm. longa. Stamina numerosissima (in flore uno 187 numerata), usque 6.5 mm. longa. Antherae 0.5 mm. longae. Ovarium late ellipsoideum, 3 mm. longum; styli 3, fere recti, crassi, divergentes, 1.1 mm. longi.

TYPE, *Cuatrecasas 10139*, collected on the Paramo de Arcabuco between Arcabuco and Tunja, Boyacá, Cordillera Oriental, Colombia, and deposited in the Britton Herbarium of the New York Botanical Garden. The cordate-clasping leaves, the large number of stamens, and the very short styles set *H. cuatrecasii* apart as unique among the species of the subsection *Eubrathys* known from South America.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

[1] Bull. Torrey Club **56**: 100–107. 1929; Torreya **29**: 137. 1929.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 175–181 MARCH, 1943

THE METAPHASE STAGE IN COLCHICINIZED ONION ROOT-TIPS

MICHAEL LEVINE AND SIDNEY GELBER

The lethal effects of X-ray and radium emanations on neoplastic tissues are in a large measure dependent upon the stage of development of the component cells. The dividing cell, it seems, is more vulnerable to these physical agents than the resting ones. The neoplasia of animals present many difficulties to the radium or X-ray therapeutist because of the great variations in the number of dividing cells in such tissues. Arresting cell division in the metaphase stage in neoplastic tissue of animals by the application of colchicine has revealed no constancy in the number of dividing cells, for in the individual tumor DuBilier and Warren (1941) have shown that the maximum effect of colchicine on the Brown-Pearce rabbit epithelioma is attained in 6 hours with a single dose (0.1 mg per 100 gm. body wt.); with repeated doses the colchicine attains its maximum effect at 12 hours. These results apply to an average for a given dose, yet the response of the individual tumor varies greatly. The results are so variable that these authors believe that a trial of the effect of colchicine and roentgen therapy is impracticable. This is readily understood, for in transplantable tumors the rate of growth may vary with the transplant, the host, and other factors still unknown.

The ready availability of dividing onion root-tip cells and the ease with which this tissue may be observed has led us to the study of the effect of X-ray on this tissue affected by colchicine. The arrest of the mitotic changes in metaphase exposes the cells at a stage when X-rays are supposed by many to be most effective in destroying them. It accordingly became necessary to determine at what time after treatment colchicine-treated onion roots present the greatest number of dividing cells in metaphase.

The following is a report on the number of cells in metaphase stage found in the root tips of *Allium cepa*, var. Yellow Globe, after exposure to .01 per cent colchicine solution. The regularity with which the root-tips of the onions hypertrophied after treatment with the solution of colchicine used seemed to indicate that the maximum changes occurred in about 48 hours. Cytological preparations of this tissue showed however, that the largest number of dividing cells were to be found at much shorter exposures. A systematic study was made of root tips exposed to a uniform solution of colchicine (.01 per cent) from 6 hours to 6 days. The number of resting cells and cells in the metaphase stage was counted in four root-tips selected at random after each of the following periods of exposure: 6, 9, 12, 24, 36, 48, 72, 96, 120, and 140 hours.

The effect of colchicine as it is now well established, is to arrest the mitotic division in the metaphase stage. While it was first thought that colchicine increased the number of division stages, Ludford (1936) showed that it arrested the cell in its metaphase division stage so that the number of dividing cells appeared to increase.

Ludford showed that .00001 per cent solution is effective on mitosis in some animal tissue. Levan (1938) studied the effects of various concentrations of colchicine at time varying from 7 minutes to 72 hours after the treatment. Concentration of .0055 per cent, he believed, was sufficient to cause disturbance of the spindle figure. Levine and Lein (1941) showed that a .001 per cent solution of colchicine was sufficient to arrest the elongation of roots of the onion. Levan further observed that the threshold value for affecting mitosis in roots of *Allium cepa* with colchicine lies between .005 per cent and .01 per cent solutions after an exposure of 4 hours. We selected the larger dose (.01 per cent solution) for our studies.

METHODS AND MATERIALS

The onions were drawn from regular shipments made to this institution for dietary purposes. These were selected from large numbers for uniformity of size, weight, shape, and color; the genetic constitution of the species was unknown.

The resting bulbs were placed on top of cylindrical vessels of 240 cc. capacity, filled with cool fresh water daily, so that the root end of each bulb was constantly immersed. The vessels were coated on the outer surface with a dense opaque material so as to exclude light. The bulbs were permitted to rest in water until a sufficient number of roots had been formed. After a period of from 7 to 10 days bulbs with a fair number of roots (15–20) were transferred to similar vessels filled with a .01 per cent aqueous solution of colchicine. These bulbs were labeled and placed in a moderately cool part of the laboratory with constantly subdued light. To obtain as much diversity in cell counts as possible, roots from four different bulbs were used in each test. The onions used were divided into four series each comprising from 12 to 20 bulbs. The root-tips were examined first after exposure to the colchicine solution for 6-, 24-, and 48-hour periods. Three additional groups of onions with many controls were selected from those exposed 9, 12, 36, 72, 96, 120, and 140 hours to the colchicine treatment. These were studied in the following order: 36, 120, and 140 hours of exposure, 9, 72, and 96 hours of exposure, and 12 hours of exposure.

After a given exposure to the colchicine was made, the root-tips from each onion were fixed according to Warmke's (1935) method; although fixation for greater periods than those suggested by Warmke was found necessary for root-tips exposed for long intervals. The root-tips were

stained in aceto-carmine and chlorazol black E, as described by Nebel (1940). The latter dye intensifies the stains and makes the cell- and chromosome-count more reliable. More than 4000 cells were counted in each series after exposure to colchicine for a given time, and the percentage of cells in metaphase stage was calculated. Control bulbs were grown in water at the same time for from 7 to 15 days, but not exposed to colchicine; the water was changed daily. The roots of these bulbs were fixed and smeared in the same way. More than 4000 cells were counted from this group.

CELL COUNTS IN UNTREATED BULBS

The untreated roots were a bright and glistening white. The cells of four were counted; of 4112 cells there were 3963 in resting or prophase stages and 149 in metaphase, 3.6 per cent of the total counted (Table 1). Three of the counted root-tips contained an approximately equal number of cells in metaphase stage. One root contained 58, an extreme divergence from the average. This may indicate the selection of a shorter, younger root, although the effort has been made to select for the count roots of equal length. The extreme percentages are represented in the graph (fig. 1) by broken lines, while the black line represents the average percentages of metaphase stages based on the figures given in the accompanying table.

CELL COUNTS IN TREATED BULBS

In table 1, the counts have been made from bulbs exposed to .01 per cent colchicine for 6, 9, 12, 24, 36, 48, 72, 96, 120, and 140 hours. During long exposures the colchicine solutions were not changed but fresh solution was added as required. The tips were removed, fixed, and smeared by the methods mentioned above. The cells in resting and metaphase stages were counted. Root-tips exposed to .01 per cent colchicine for 6 hours have a uniform number of metaphase stages, all but root 3F which has only 55 cells in metaphase stages against 73 in the other roots recorded (see table 1). The average percentage (6.7) of cells in the metaphase stage has almost doubled as a result of the exposure. At any time after exposure the departures from the average are approximately equal, as shown by fig. 1. In the 9-hour series, 4320 cells were counted, of which 405 were in metaphase, 9.38 per cent of the total cells counted. The variation in the number of cells in metaphase is small. The tendency to an increase of the number of metaphases is now apparent, as shown in table 1. This tendency became obvious when the counts for the different periods of exposures were arranged chronologically. Among roots exposed for 12 hours, the difference between roots 2T and 5T is 35 cells in metaphase; approximately equal to the difference between extremes in the untreated roots. The number of metaphase stages in this series totals 490 in 4195 cells counted (11.6 per cent) as against 405 in 4320 cells

TABLE 1. *Number of cells in metaphase in untreated roots and in roots treated with .01 per cent colchicine*

Exposure	Root	Cells counted	Cells in metaphase	Per cent cells in metaphase
None	3	1026	26	2.53
	1B	1017	34	3.34
	2B	1043	58	5.56
	3B	1026	31	3.02
		4112	149	3.62
6 hours	2F	1016	73	7.18
	3F	1026	55	5.36
	4F	1019	71	6.96
	5F	1021	76	7.44
		4082	275	6.74
9 hours	2H	1109	107	9.64
	3H	1036	105	10.13
	5H	1143	96	8.39
	6H	1032	97	9.39
		4320	405	9.38
12 hours	2T	1149	143	12.44
	3T	1031	116	11.25
	4T	1011	123	12.16
	5T	1044	108	10.34
		4195	490	11.68
24 hours	1E	1034	156	15.08
	2E	1232	204	16.55
	3E	1022	156	15.45
	4E	1010	121	11.98
		4298	637	14.88
36 hours	5X	1210	101	8.34
	6X	1170	104	8.88
	9X	1045	102	9.76
	10X	1041	116	11.14
		4466	423	9.47
48 hours	2C	1057	85	8.04
	3C	1097	96	8.75
	4C	1002	75	7.48
	6C	1026	80	7.79
		4182	336	8.03
72 hours	6Z	1109	60	5.40
	7Z	1062	61	5.74
	8Z	1117	84	7.52
	10Z	1123	70	6.23
		4411	275	6.23
96 hours	3V	1110	39	3.51
	4V	1053	23	2.18
	5V	1039	45	4.33
	7V	1084	53	4.88
		4286	160	3.73
120 hours	2Q	1195	46	3.84
	5Q	1028	33	2.99
	6Q	1050	28	2.66
	7Q	1235	55	4.45
		4508	162	3.59
140 hours	3L	1125	33	2.93
	5L	1023	24	2.34
	6L	1034	53	5.12
	8L	1081	16	1.38
		4263	125	2.93

counted (9.3 per cent) after the 9-hour treatment and 275 in 4082 cells counted (6.7 per cent) after the 6-hour treatment. It appears that some

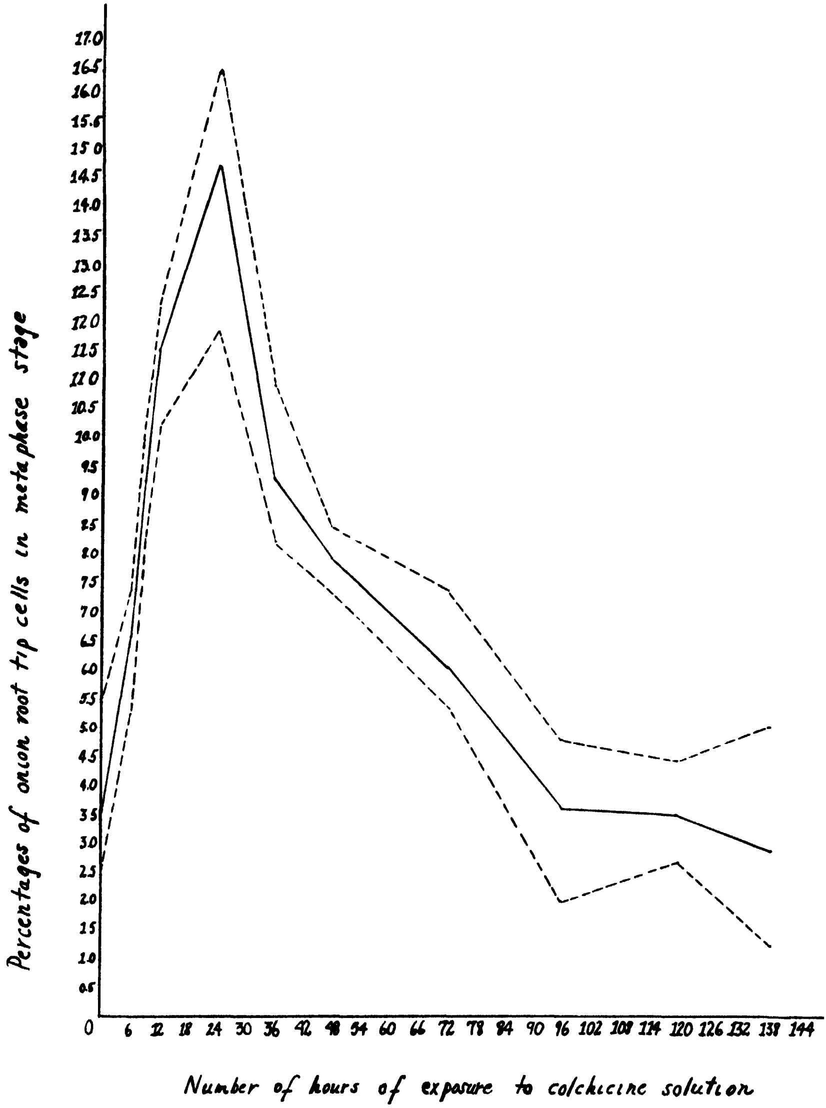


FIG. 1. The percentages of cells in metaphase in the root tips of *Allium cepa*; untreated and exposed to a solution of .01 per cent colchicine for from 6 to 140 hours. Middle line indicates average percentage; upper broken line indicates maximum percentage; lower broken line indicates minimum percentage.

roots attain the maximum number of metaphase stages after this exposure, as root 2T.

Of a total of 4298 cells counted in root-tips exposed for 24 hours to the same concentration of colchicine 637 cells were found in metaphase. This is an increase of 11.2 per cent metaphases over the number counted in the untreated root-tips and an increase of 3.2 per cent over the 12-hour-treated root tips. The 24-hour exposure seems to yield the maximum effect with .01 per cent solution of colchicine. From a study of figure 1 it is clear that the greatest extremes, in the number of metaphases also occur here. It appears that it represents for some roots the critical exposure, for in the following treatments a definite decrease in the number of metaphase stages is met, as shown by table 1. After the 36-hour exposure there are fewer metaphases; from 637 of 4298 cells for the 24-hour period to 423 of 4466 cells (9.4 per cent). The extremes are represented by 101 metaphases in 1210 cells counted in root 5X and 116 metaphases in 1041 cells counted in root 10X, a difference of 2.8 per cent. In this series the results may be interpreted as a toxic effect on cells in the resting stages. Some of the cells in the metaphase stage may have completed their nuclear reconstruction, or some may have degenerated.

In root-tips exposed for 48 hours to .01 per cent colchicine there are still fewer metaphases than in those exposed for 36 hours. The continued exposures observed after 72, 96, 120, and 140 hours showed a gradual decline in the percentage of cells in metaphase, until in the latter exposures we have an average percentage of metaphases slightly lower than that of the untreated roots (see graph). From the 96-hour to the 140-hour exposures the differences between extremes are approximately uniform; especially is this noted in the 120-hour-treated roots. The number of metaphases counted in roots exposed for 96 and 120 hours are 160 and 162, respectively, from counts of 4286 cells in the 96-hour exposure and 4508 cells in the 120-hour series. In the roots exposed for 140 hours the number of cells in mitosis is 125 in 4263 cells counted. The average percentage for the 140-hour period is 2.9, which is slightly lower than that observed for the untreated roots.

It appears from these studies that colchicine in a given concentration for a given period up to and including 24 hours increases the number of metaphase stages in the root-tips of the onion. The variations in individual responses for a given solution and a given period are approximately from 1 per cent to 3 per cent of the average for all the series.

It is clear that in these experiments .01 per cent colchicine has an inhibiting effect on the development of the prophase stage after the 24th hour. The extreme variation as shown in the graph indicates the beginning of the toxic effects exerted by the colchicine. This may be expressed in the increased toxic influence of the colchicine or the inability of the colchicine to keep the dividing cells in metaphase any longer. Both conditions seem to prevail. The colchicinized cells begin to degenerate; comparatively large lobulate nuclei are formed. In a subsequent report effects of a study of 900–3000 roentgen ray units on colchicinized root tips will be given.

SUMMARY

1. Onion root-tips grown in water for 10–15 days contain an average of 3.6 per cent cells in metaphase stage.

2. Roots exposed to .01 per cent colchicine from 6 to 24 hours contain a gradually increasing percentage of cells in metaphase which reaches the maximum at 24 hours.

3. Continued exposure for longer than 24 hours shows a gradual decline in the number of mitotic stages to a point slightly below the figure observed for the untreated root-tips.

4. The differences between extremes in the number of metaphase stages in untreated and in all colchicinized root-tips are approximately the same except at the critical exposures, shown here to be 24 hours with .01 per cent colchicine, where the variation is the greatest.

5. The number of metaphases in the colchicinized root-tips is predictable within the limits of variation of the 24-hour treatment as given here.

6. It appears that simple plant structures like the onion root-tip are suitable for the initial studies of the combined effects of colchicine and x-rays.

LABORATORY DIVISION, MONTEFIORE HOSPITAL
NEW YORK

Literature Cited

Dermen, Haig. 1940. Colchicine, polyploidy, and technique. Bot. Rev. **6:** 599–635.

Dubilier, Benjamin, & Warren, Stafford L. 1941. The effect of colchicine on the mitotic activity of the Brown Pearce rabbit epithelioma. Cancer Research **1:** 966–969.

Levan, Albert. 1938. The effect of colchicine on root mitoses in *Allium*. Hereditas **24:** 471–486.

Levine, Michael, & Lein, Joseph. 1941. The effects of various growth substances on the number and the length of roots of *Allium cepa*. Am. Jour. Bot. **28:** 163–168.

Ludford, R. J. 1936. The action of toxic substances upon the division of normal and malignant cells *in vitro* and *in vivo*. Arch. Exp. Zellforsch. **18:** 411–441.

Nebel, B. R. 1940. Chlorazol black E as an aceto-carmine auxiliary stain. Stain Technol. **15:** 69–72.

Warmke, H. E. 1935. A permanent root tip smear method. Stain Technol. **10:** 101–103.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 182–183 MARCH, 1943

DIFFERENTIATION IN RED ROOT-TIPS OF PHALARIS ARUNDINACEA

ROBERT BLOCH

Molisch[1] described the interesting occurrence of red root-tips in a number of plant families (Crassulaceae, Saxifragaceae, Balsaminaceae, Melastomaceae, Compositae); it was stated that the coloration was due to the presence of anthocyanin in the youngest part of the meristems and in the root-cap cells, but no further histological details were given.

During studies of developing roots of various genera of small-seeded grasses, the author noted frequent occurrence of a red coloration in root-tips of *Phalaris arundinacea*. The seeds were grown on damp lens paper in moist chambers with the new technique[2] for observation of living plant meristems at successive intervals. In the present study seeds were germinated either in light or in darkness, and red root-tips made their appearance after approximately four days.

Microscopic investigation of the living root showed that the entire meristematic area as well as the cells of the root-cap were intensely colored. The distribution of the pigment was always associated with a dense protoplasmic condition in the cells, but as the cells begin to vacuolate, at a distance of about 250–400 micra from the apex, the coloration becomes less conspicuous. At the last cell division in the basal portion of the meristem, two types of cells are set apart in the surface of the root; they are trichoblasts which later develop root-hairs, and ordinary surface cells which remain hairless. In *Phalaris arundinacea* these two cell types roughly alternate, though occasionally several hairless cells may occur in direct succession. Trichoblasts and hairless cells can first be distinguished by slight differences in the rate of longitudinal expansion (lower in the trichoblast), but in this genus the dissimilarity is made much more conspicuous by a difference in the depth of color, the trichoblast not only remaining more densely protoplasmic, but also more intensely colored; this condition often persists until the root-hair cell has reached considerable length (fig. 1). Even later some pigmentation was frequently noted still associated with the aggregation of cytoplasm at the base or the tip of the growing root-hair, which develops either at the apical end of the cell or somewhat more toward its middle. The much more rapidly expanding and finally considerably longer hairless cells, on the other

[1] **Molisch, H.** Rote Wurzelspitzen. Ber. Deuts. Bot. Ges. **46**: 311–317. 1928.

[2] **Sinnott, E. W.** Growth and differentiation in living plant meristems. Proc. Nat. Acad. **25**: 55–58. 1939. **Sinnott, E. W. & Bloch, R.** Changes in intercellular relationships during the growth and differentiation of living plant tissues. Am. Jour. Bot. **26**: 625–634. 1939.

hand, lose their dense cytoplasmic condition and their pigmentation at a much earlier stage (fig. 1).

The differences in the degree of pigmentation are obviously an expression of physiological, metabolic differences between trichoblasts and hairless cells in the transition zone located between the terminal meristem and the vacuolate, mature region of the root. The natural red pigmentation may serve as a tool in distinguishing without difficulty at a very early stage of differentiation the two types of cells in a living, undisturbed condition; it is equally of assistance in following their development in the region of vacuolation and maturation, and it makes it especially easy to identify the same cells when repeated observations of the same root tips are made.

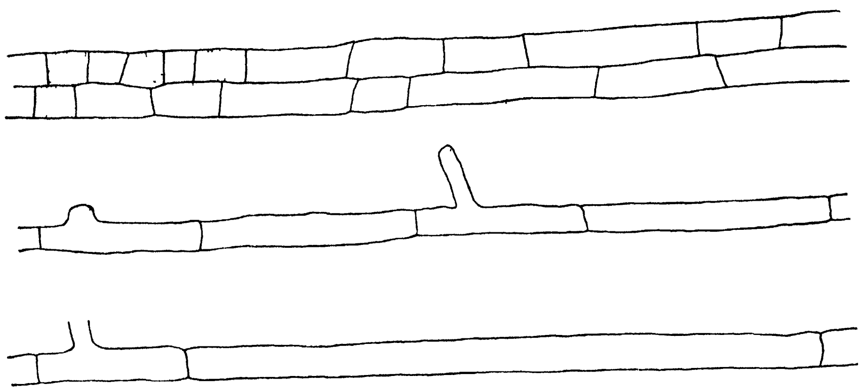


FIG. 1. *Phalaris arundinacea*. Surface of living root, showing unequal growth and the progressive loss of coloration in naturally pigmented trichoblasts (darker) and alternating hairless cells (lighter), in zones of beginning vacuolation (above) and maturity (below). × 250.

Generally the central portion of the densely protoplasmic cells appears lighter colored, indicating the position of the colorless nucleus. The color-giving pigment is apparently distributed in small vacuoles throughout dense aggregates of cytoplasm and becomes less conspicuous as general vacuolation proceeds in the cells; the color fades out first in the rapidly expanding hairless cells. The metabolically much more active trichoblasts retain much longer a considerable amount of cytoplasm and pigment, though these also progressively diminish. It follows that a trichoblast compared with an even younger hairless cell which has the same size may show a denser cytoplasmic content and a deeper pigmentation.

It was noted that in injured roots the coloration in the cytoplasm becomes at first more intense as a result of necrobiotic changes. As degeneration proceeds, however, the color is frequently taken up by the nucleus, which then turns darkish red.

OSBORN BOTANICAL LABORATORY
YALE UNIVERSITY

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 184–189 MARCH, 1943

FURTHER EXPERIMENTS ON THE NUTRITION OF ISOLATED TOMATO ROOTS[1]

JAMES BONNER

INTRODUCTION

The exact accessory growth substance requirements of isolated tomato roots are at present in dispute. It is agreed by all the workers in the field that thiamine or a constituent portion or portions thereof are required. Robbins and Schmidt (1939 a, b) and Robbins (1941) have shown further that pyridoxine exerts a powerful growth-promoting influence on the growth of the isolated tomato root, a conclusion confirmed by Bonner and Devirian (1939), Bonner (1940), and Day (1941). White (1940) finds however that isolated tomato roots are not affected in their growth by pyridoxine but do respond to glycine (1939, 1940). Bonner and Devirian (1939) and Bonner (1940) could not establish any important effect of glycine but did find that in the presence of adequate amounts of thiamine and pyridoxine isolated tomato roots responded with increased growth to the addition of nicotinic acid. Neither Robbins and Schmidt (1939b) nor White (1940) confirmed this activity of nicotinic acid. Robbins (1941) has however later shown that different strains of isolated tomato roots vary greatly in their response to nicotinic acid, some responding vigorously and some responding little. The present work confirms Robbins and shows that closely related clones vary in their responses to nicotinic acid. In addition the responses of four clones of tomato roots to glycine are here reported.

METHODS

Each of the clones of isolated tomato roots discussed below was derived from an individual seed of *Lycopersicon esculentum*, var. "San Jose Canner." The seeds were disinfected in 0.1 per cent $HgCl_2$, and laid out to germinate in aseptic Petri dishes. When the seedling roots had attained a length of 2–3 cm. the terminal 10 mm. of root was removed and cultivated in 10 cm. Petri dishes containing 25 cc. of nutrient solution. The nutrient solution contained per liter of Pyrex-redistilled water: 236 mgs. $Ca(No_3)_2 \cdot 4H_2O$, 36 mgs. $MgSO_4 \cdot 7H_2O$, 81 mgs. KNO_3, 65 mgs. KCl, 20 mgs. KH_2PO_4, 1.5 mgs. ferric tartrate, and 20 gms. sucrose, with 0.1 mgs. thiamine, 0.5 mgs. nicotinic acid, and 0.1 mgs. pyridoxine as addenda. During the course of the experiments numerous trials were made in an effort to improve the consti-

[1] Report of work done with the assistance of the Work Projects Administration O. P. 365–1–07–2.

tution of the basic nutrient solution but no alteration of the amount of any chemical resulted in significant increase of root growth. Glycine where used was added at the rate of 3 mgs. per liter as recommended by White (1939, 1940). The roots were incubated in the dark at 25° C for one week and were then subcultured by removal of 1 cm. branch root-tips to fresh medium. This procedure of subculture and transfer was used in each subsequent transfer, which occurred at regular weekly intervals. At the end of each transfer period, the growth in length of the principal axis of each root was measured. The growth measurements presented below are averages of such measurements.

During the prosecution of this work, no piece of glassware which came in contact with a solution other than distilled water was used a second time without an intervening cleaning in sulfuric acid–potassium dichromate cleaning solution followed by seven or more rinsings in tap and distilled water, a precaution which has been observed in this laboratory since the initiation of isolated root culture work.

OBSERVATIONS

Uniformity of Material. Two hundred branch root-tips, randomly divided into 10 lots of 20 tips each, were used as the innocula for most of the experiments recorded below. Table 1 shows the degree of uniformity attained in a typical dummy experiment of this kind. Of the 20 initial tips, from 18 to 20 grew in the various groups. With respect to growth in length, the average deviation of the group means from the average of the group means was 3.8 per cent. Treatment of the data by the analysis of variance shows that the groups are homogeneous and do not differ significantly among themselves. The best estimate of the standard error of one group mean of 20 is 2.72 and correspondingly a minimum difference of about 20 per cent between two

TABLE 1

Uniformity trial with 200 one cm. branch root tips of isolated tomato roots (Clone W). Figures represent growth of principal root axis in mm. in 7 days

Group	Number of tips used	Number of tips which grew	Av. growth mm.	Std. error of av. growth
1	20	20	51.8	1.96
2	20	20	54.2	3.04
3	20	18	50.0	1.81
4	20	18	50.6	2.35
5	20	18	55.3	3.06
6	20	18	50.3	1.74
7	20	19	52.4	2.71
8	20	20	53.8	3.52
9	20	18	54.4	3.70
10	20	20	56.8	3.04

group means of 20 might be expected to be significant at the 1 per cent level. The work reported here is based on a series of 48 experiments generally similar in plan to that given in table 1.

Response to Various Growth Substances. In these experiments roots were cultivated for one week in nutrient solutions containing various addenda. The roots were then subcultured and cultivated for a second week in similar nutrient. Table 2 gives data on the growth, in this second transfer,

TABLE 2

Response of 3 different clones of isolated tomato roots to 6 different nutrient solutions

Added growth substances	Clone A	Clone H		Clone W	
	Expt. *G–44*	*G–33*	*G–34*	*G–31*	*G–41*
	Growth in mm. per root per week				
None	0.0	0.0	0.0	0.0	0.0
B_1 alone	0.0	0.0	0.0	0.0	0.0
$B_1 + B_6$	31.2 ± 1.58	31.3 ± 2.83	30.9 ± 2.37	46.4 ± 2.79	49.8 ± 2.55
B_1 + nicotinic acid + B_6	34.1 ± 1.60	40.3 ± 1.90[a]	38.8 ± 2.34[b]	44.3 ± 2.94	46.8 ± 1.91
Glycine alone	0.0	0.0	0.0	0.0	0.0
	G–43	*G–36*	*G–40*	*G–39*	*G–42*
None	0.0	0.0	0.0	0.0	0.0
B_1 alone	0.0	0.0	0.0	0.0	0.0
$B_1 + B_6$	48.4 ± 1.92	30.9 ± 1.28	28.2 ± 1.94	50.2 ± 2.22	49.4 ± 2.24
B_1 + nicotinic acid + B_6	50.0 ± 1.38	39.3 ± 2.06[a]	37.2 ± 1.35[a]	50.0 ± 2.28	46.0 ± 2.13
B_1 + glycine	0.0	2.5 ± 0.39	0.0	0.0	0.0

[a] Increase in growth rate associated with nicotinic acid significant at 1% level.
[b] Increase in growth rate associated with nicotinic acid significant at 5% level.

of three different clones in six different nutrient solutions. In no case was appreciable growth obtained in basic nutrient solution alone, in basic nutrient solution plus thiamine, or in basic nutrient solution plus glycine. In one experiment a slight response to thiamine plus glycine was obtained, but this could not be repeated in other experiments with the same clone. In every experiment thiamine plus pyridoxine supported good growth, whereas thiamine plus glycine elicited little or no growth. With these clones then, and with four additional clones of "San Jose Canner" roots for which detailed data will not be given, glycine does not appear capable of replacing pyridoxine, a conclusion in general agreement with that of Robbins. In other experiments, the influence of glycine in the presence of varied thiamine concentrations was investigated. In no case was response to glycine found.

Of the clones used in the experiments of table 2 only clone H responded significantly to the addition of nicotinic acid. This difference between the behavior of clone H and the other two clones (A and W) has been confirmed in 7 further experiments and it seems logical to conclude that individual

clones vary in their response to nicotinic acid. This conclusion is again in agreement with that of Robbins (1941).

One-Month Transfer Periods. The cultural conditions used by the present author differ in numerous ways from those used by Robbins and by White. Petri dishes rather than Erlenmeyer flasks are used as culture vessels and transfer periods of one week, following White, are used rather than the 1–2-month transfer periods used by Robbins. In one series of experiments therefore, tomato roots were grown in 125 cc. Erlenmeyer flasks, 50 cc. of nutrient per flask. The flasks were inoculated with basal fragments of vigorous roots and incubated in diffuse light for one month. These roots were then subcultured and incubated for a second month in fresh medium, after which the procedure was repeated for a third time. After each transfer dry-weight measurements (as used by Robbins) were made as well as linear growth measurements. Twenty roots of clone II (table 2) were measured and weighed in each treatment given in table 3, which presents data from the third monthly transfer. It is apparent that with this clone growth responses both to pyridoxine and to nicotinic acid were obtained under these conditions and that these responses were qualitatively similar to those obtained in Petri dish culture with one-week transfer periods. The responses are evident from the dry-weight measurements as well as from the linear measurements.

TABLE 3

Growth of roots of clone II in Erlenmeyer flasks during a transfer period of 1 month. Each mean is based on twenty roots

Growth substances in nutrient:	None	Thiamine	Thiamine + pyridoxine	Thiamine + pyridoxine + nicotinic acid
Av. growth mm. per root	0.0	5.2 ± 2.45	22 ± 5.75	58 ± 2.34
Av. dry wt. per root; mgs.	0.0	0.18 ± .09	2.0 ± 0.48	7.3 ± 0.28

Small but definite growth in solutions containing thiamine as the sole added growth substance was observed in all three passages of this experiment. It appears quite possible that the same slow growth takes place in thiamine cultures of the present clones when these clones are transferred weekly but that owing to the small increments such growth can be detected only with difficulty.

Clone of P. R. White. Through the courtesy of Dr. P. R. White, samples of the standard White clone of isolated tomato roots were obtained on two occasions. In a typical experiment with this clone, of 44 roots maintained in thiamine–glycine medium all ceased growth within 3 transfers. Of 14 roots maintained in thiamine–nicotinic acid–pyridoxine medium all grew satis-

factorily and made an average increment of 32 mm. per root per week. It would appear that the White clone under the conditions used by the present author cannot be maintained in a thiamine–glycine nutrient medium.

DISCUSSION

The present work was undertaken in an effort to find answers to two questions: (1.) The reason for the discrepancy in the results of Robbins and those of Bonner as to the effectiveness of nicotinic acid as a growth substance for isolated tomato roots; and (2.) the reason for the discrepancy between the results of Robbins and Bonner on the one hand and those of White on the other as to the effectiveness of pyridoxine and glycine as growth substances for isolated tomato roots. As to nicotinic acid, it has now been shown both by Robbins and in the present paper that response to nicotinic acid (in the presence of thiamine and pyridoxine) is a property which varies with different clones or strains of isolated tomato roots. Some strains respond while others do not. Although the cultural conditions and the criteria of growth used in the two laboratories are different, still response to nicotinic acid can be determined, with suitable strains, in both laboratories. With regard to glycine, however, it does not seem probable that the different results obtained are due to metabolic differences in the clones used. Of 14 clones of isolated tomato roots which have been investigated by the present author, not one has been found in which glycine is able to replace pyrixodine, or in which glycine has yet been found to have any important growth effect. It would seem more probable that the effect of glycine is obtained under conditions peculiar to some laboratories and not found in other laboratories. Thus White (1940) found that Robbins' standard clone, when grown in White's laboratory, failed to respond to pyridoxine, but did respond to glycine although to a lesser extent than the White standard clone. White's standard clone as grown in this laboratory failed to respond to glycine in the presence of thiamine but did make satisfactory growth in thiamine–pyridoxine–nicotinic acid nutrient medium. It should be recalled also that White (1939) has found that sunflower roots make continued luxuriant growth in thiamine–glycine medium. In this laboratory sunflower roots were found to respond primarily to thiamine and pyridoxine (1940).

SUMMARY

1. Of three clones of isolated tomato roots reported in the present paper, all were found to grow luxuriantly through repeated transfers in nutrient solution containing thiamine and pyridoxine as accessory growth substances. None of the strains made continued growth in nutrient solution containing thiamine and glycine as accessory growth substances.

2. Of the three clones, one responded with increased growth when nico-

tinic acid was added to the medium in addition to thiamine and pyridoxine. The other two clones did not respond to nicotinic acid.

CALIFORNIA INSTITUTE OF TECHNOLOGY
PASADENA, CALIFORNIA

Literature Cited

Bonner, J. On the growth factor requirements of isolated roots. Am. Jour. Bot. **27:** 692–701 1940.

Bonner, J. & Devirian, P. Growth factor requirements of four species of isolated roots. Am. Jour. Bot. **26:** 661–665. 1939.

Day, Dorothy. Vitamin B_6 and growth of excised tomato roots in agar culture. Science **94:** 468–469. 1941.

Robbins, W. J. Growth of excised roots and heterosis in tomatoes. Am. Jour. Bot. **28:** 216–225. 1941.

———. Specificity of pyridoxine for excised tomato roots. Am. Jour. Bot. **29:** 241–245. 1942.

Robbins, W. J. & Schmidt, M. Vitamin B_6 a growth substance for excised tomato roots. Proc. Nat Acad **25:** 1–3. 1939a.

———. Further experiments on excised tomato roots. Am. Jour. Bot. **26:** 149 159. 1939b

White, P. R. Glycine in the nutrition of excised tomato roots. Plant Physiol. **14:** 527–538. 1939.

———. Vitamin B_6, nicotinic acid, pyridine, glycine and thiamin in the nutrition of excised tomato roots. Am. Jour. Bot. **27:** 811 821. 1940.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 2, pp. 190–197 MARCH, 1943

THE RELATION OF CERTAIN FUNGI TO THIAMINE

WILLIAM J. ROBBINS AND ROBERTA MA

The discovery that certain fungi, incapable of growing on a basal medium, developed when traces of thiamine were added was followed by the observation that the growth-substance deficiency of some of them could be satisfied by substituting for thiamine its pyrimidine and thiazole intermediates.[1] This observation was interpreted in two ways.

On the one hand, it was assumed that thiamine was essential for all fungi. Some were autotrophic as far as this vitamin was concerned and synthesized it from elementary foods and minerals. Others were incapable of this synthesis and suffered from a thiamine deficiency which necessitated a supply of this vitamin in the nutrient medium. Those belonging to the group which grew in the presence of one or both intermediates were considered capable of synthesizing the essential thiamine from its intermediates and some of them were believed capable of making one of the intermediates as well. Robbins and Kavanagh (16) and Robbins (15) presented this point of view.

Other investigators, however, were inclined to believe that thiamine as such was not effective but owed its activity to some indirect action or to its intermediates. Schopfer and Jung (11) concluded that the action of thiamine on *Phycomyces* was indirect; its presence was considered indispensable for the synthesis by the fungus of factors peculiar to it. Schopfer and Jung (12) inclined toward the idea that *Phycomyces* split the thiamine molecule into its intermediates and used these for different purposes. Müller and Schopfer (3) believed that *M. ramannianus* probably split the thiamine molecule and utilized the thiazole portion. Schopfer (6) in studying the thiamine deficiencies of *Rodotorula* sp. concluded that these organisms split the thiamine molecule, thus liberating the thiazole or the pyrimidine which they required. Schopfer (7) admitted as a hypothesis that thiamine might be synthesized by fungi from its constituents but considered that the situation may vary with the organism.

The discovery that various species of *Phytophthora* needed molecular thiamine and failed to grow when furnished the intermediates, made possible a bioassay for thiamine (13, 14). By employing *Phytophthora cinnamomi* as a test organism Bonner and Buchman (2) demonstrated the synthesis by *Phycomyces* of thiamine from its intermediates. By using the same method of assay Schopfer (8) confirmed this observation and showed that

[1] The terms pyrimidine and thiazole as used here refer to 2-methyl-5-bromo-methyl-6-aminopyrimidine and 4-methyl-5-β-hydroxyethyl thiazole respectively. These are the two intermediates of thiamine.

Rhodotorula rubra grown on pyrimidine alone and *Mucor ramannianus* grown on thiazole alone also synthesized thiamine. Schopfer and Blumer (9) showed that *Schizophyllum commune*, which requires pyrimidine only as a supplement, formed thiamine in such a medium. From these reports, and those of others, it appears probable that the first of the interpretations presented above on the relation of fungi to thiamine is the more nearly correct.

In surveying the relation of species of *Ceratostomella* and other fungi to vitamins, several were found to suffer from thiamine deficiencies (18, 19, 20). It appeared worth while to determine for the members of this group the kind of thiamine deficiency concerned, and in view of the earlier differences in opinion to learn also whether thiamine or a physiologically equivalent substance was produced by those capable of growing on media supplemented by one or both intermediates.

METHODS AND MATERIALS

The fungi investigated were *Ceratostomella fimbriata*, *C. ips* No. 255, *C. microspora* No. C 109, *C. montium* No. C 424, *C. obscura* No. C 104, *C. penicillata* No. C 110, *C. piceaperda* No. 240, *C. pini* No. 416, *C. pini* No. 512, *C. radicicola* No. B 261, *C. stenoceras* No. 107, *Ceratostomella* from the London plane tree (*CLP*), *Chalaropsis thielavioides* No. C 117, *Endoconidiophora* (*Ceratostomella*) *paradoxa* No. 116, *Mucor ramannianus*, and *Polyporus versicolor* No. 71700 R.

Each organism was grown in triplicate in test tubes at 20° C on a basal solution solidified with 1.5 per cent purified agar[2] and supplemented with 5 mμ moles of pyridoxine and 0.05 μg. of biotin methyl ester, and on the same medium plus per tube 10 mμ moles of thiamine, of pyrimidine and thiazole, of pyrimidine, or of thiazole. Each test tube contained 8 ml. of medium.

All media were sterilized by autoclaving at 13 lbs pressure for 20 minutes. The thiamine and pyridoxine were Merck's synthetic and the pyrimidine and thiazole[3] were supplied by the same company. The asparagine was purified by treatment with Norit A and recrystallization from alcohol. The biotin methyl ester was obtained from the SMA corporation.

OBSERVATIONS

Types of Response to Thiamine and its Intermediates. Four of the fifteen fungi tested proved to be unable to use the intermediates but required

[2] The basal solution contained per liter 50 g. dextrose, 1.5 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7H_2O$, and 2 g. asparagine. To this solution the following trace elements were added in p.p.m. 0.005 B, 0.02 Cu, 0.1 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn. The agar was purified by extraction with 5 per cent pyridine followed by 0.1 N HCl and neutralization with $Ca(OH)_2$.

[3] Some samples of thiazole are contaminated with pyrimidine. We have been furnished such samples and have had reports to this effect from three other investigators.

thiamine as such. These were *Ceratostomella fimbriata*, *CLP*, *C. penicillata*, and *Chalaropsis thielavioides*. The response of *CLP*, typical of this group, is shown in figure 1 A after 15 days growth on the basal agar medium and on that supplemented with thiamine, the two intermediates, pyrimidine, or thiazole.

Five of the fifteen fungi grew satisfactorily on the basal medium supplemented with thiamine, or with the two intermediates, but failed to grow when the supplement was limited to pyrimidine or to thiazole. These fungi were *Ceratostomella ips*, *C. pini* No. 416 and No. 512, *C. radicicola*, and

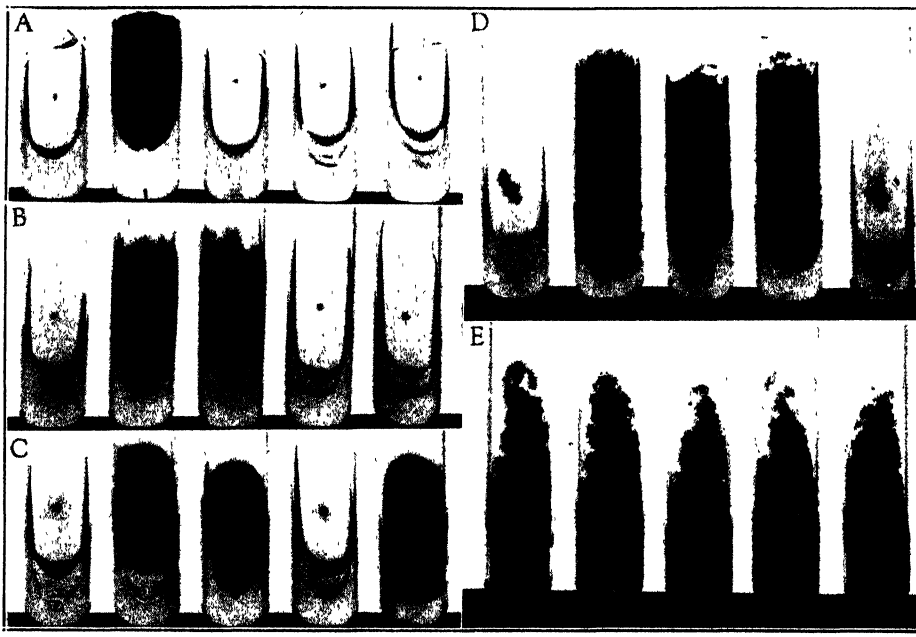


FIG. 1. Types of thiamine deficiency. Each fungus grown on a basal medium supplemented as follows: from left to right, nothing, thiamine, thiazole and pyrimidine, pyrimidine, thiazole. A, *Ceratostomella* from London plane tree; B, *Ceratostomella pini*; C, *Mucor ramannianus*; D, *Ceratostomella montium*; E, *Aspergillus niger*.

Polyporus versicolor. As far as could be judged from the growth on the agar slants, the two intermediates were as satisfactory as thiamine for these fungi. The growth of a typical representative of this group, *C. pini* No. 512, six days old, is shown in figure 1 B.

Six of the fungi grew on media supplemented with thiamine, with the two intermediates, or with pyrimidine, but did not grow on the basal medium or on the medium supplemented with thiazole. These fungi were *C. microspora*, *C. montium*, *C. obscura*, *C. piceaperda*, *C. stenoceras*, and *Endoconidiophora paradoxa* (fig. 1 D).

None of the fifteen showed a response like that of *M. ramannianus* (fig. 1 C) which grows on media supplemented with thiazole, but not on those supplemented with pyrimidine.

Quantitative Relations. The effect of various amounts of thiamine on the growth of *CLP* and *Endoconidiophora paradoxa* was studied briefly. These two fungi were grown in triplicate in test tubes containing 8 ml. of the basal agar medium supplemented per tube with 5 mμ moles of pyridoxine, 0.05 μg. of biotin, and 2 mg. of casein hydrolysate plus thiamine as follows: none, 0.001, 0.01, 0.025, 0.05, 0.075, 0.1, 0.25, 0.5, 0.75, or 1.0 mμ mole. At the end of eleven days the growth of *CLP* had covered the slopes in those tubes containing 0.25 mμ mole or more of thiamine. With smaller amounts growth was decreased (fig. 2). The effect of 0.001 mμ mole of thiamine was slight but visible. Under our experimental conditions 0.001 mμ mole of thia-

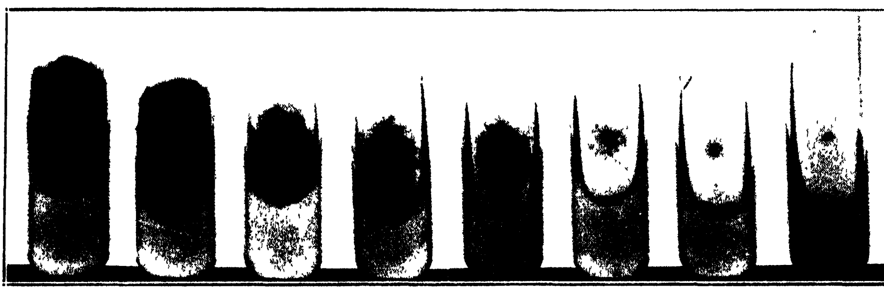


FIG. 2. Quantity of thiamine and *CLP*. From left to right, basal medium plus mμ moles of thiamine as follows: 0.5, 0.25, 0.1, 0.05, 0.025, 0.01, 0.001, none. Age, 11 days.

mine was slightly but detectably beneficial to *CLP* and quantities of 0 5 mμ mole or greater appeared to give the maximum benefit.

For *E. paradoxa* an effect of 0.001 mμ mole of thiamine was not observed, but 0.01 mμ mole was slightly beneficial. The growth increased in extent and heaviness up to 0.075 mμ mole of thiamine per tube.

While the growth of *CLP* or *E. paradoxa* on slants of an agar medium properly prepared could be used for approximating the quantity of thiamine in a substance to be assayed, the method is time-consuming and approximate only. It is doubtful whether further refinement would be desirable.

The daily growth rate in mm. of *Phycomyces blakesleeanus*, two strains of *E. paradoxa* (No. C 116 and No. B 520), and *C. radicicola* was determined in tubes in the presence of various amounts of thiamine after the method described by Beadle and Tatum (1). Fifteen ml. of the basal agar medium supplemented with pyridoxine, biotin and casein hydrolysate and quantities of thiamine ranging from 0,001 to 0.5 mμ mole were used per tube. In our experiments the growth rate of none of the fungi mentioned was sufficiently

correlated with the quantity of thiamine to suggest that it could be successfully used for determining thiamine by this method.

Synthesis of Thiamine from the Intermediates. The synthesis of thiamine by the fungi which grew on media containing the two intermediates was determined as follows:

Each fungus was grown in duplicate in 125 ml. Erlenmeyer flask containing 25 ml. of the basal solution supplemented per flask with 10 mμ moles of pyridoxine, 0.05 μg. of biotin, and 10 mμ moles each of pyrimidine and thiazole. Some flasks containing the same solution were retained uninoculated. After a moderate amount of growth had developed in the inoculated flasks (after from 5 to 14 days), acid produced by the fungus was neutralized with dilute KOH, sufficient purified agar was added to make a 1.5 per cent solution, and the flasks were autoclaved. At the same time agar was added to the uninoculated solutions which also were autoclaved. Both the check medium and that in which the fungus under investigation had grown were then inoculated with *CLP*. Since this organism does not grow unless the culture medium contains molecular thiamine, its development demonstrated the presence of thiamine or a physiologically equivalent substance. *C. ips*, the two strains of *C. pini*, *C. radicicola*, and *Polyporus versicolor* were found to produce appreciable quantities of thiamine when grown in liquid media supplemented with thiazole and pyrimidine.

In this method both the mycelium and the liquid in which the fungus under investigation grew were included in the final test medium. It is not possible to say whether the thiamine which was produced was retained by the fungus mycelium or excreted in part into the surrounding liquid.

Synthesis of Thiazole and Thiamine. The synthesis of thiazole[4] by those fungi which grew in a solution supplemented with pyrimidine was demonstrated by a procedure similar to that used in testing for thiamine production. However, the fungus investigated was grown in the basal solution supplemented with pyridoxine, biotin, and pyrimidine. *M. ramannianus* was used as a test organism for thiazole. The synthesis of thiamine also was determined for this group by using *CLP*.

Each of the six fungi which grew in solutions supplemented with pyrimidine only were found to produce thiazole and thiamine in a liquid medium supplemented with pyrimidine (fig. 3).

Synthesis of Pyrimidine and Thiamine. The synthesis of pyrimidine and thiamine by *M. ramannianus* was demonstrated by cultivating the fungus in the basal solution supplemented with thiazole. *E. paradoxa* was the

[4] The bioassays used in this investigation do not prove the presence of free thiazole or free pyrimidine.

test organism employed for pyrimidine and *CLP* for thiamine. Appreciable quantities of both pyrimidine and thiamine were found to be produced by *M. ramannianus* when grown in the basal solution supplemented with thiazole.

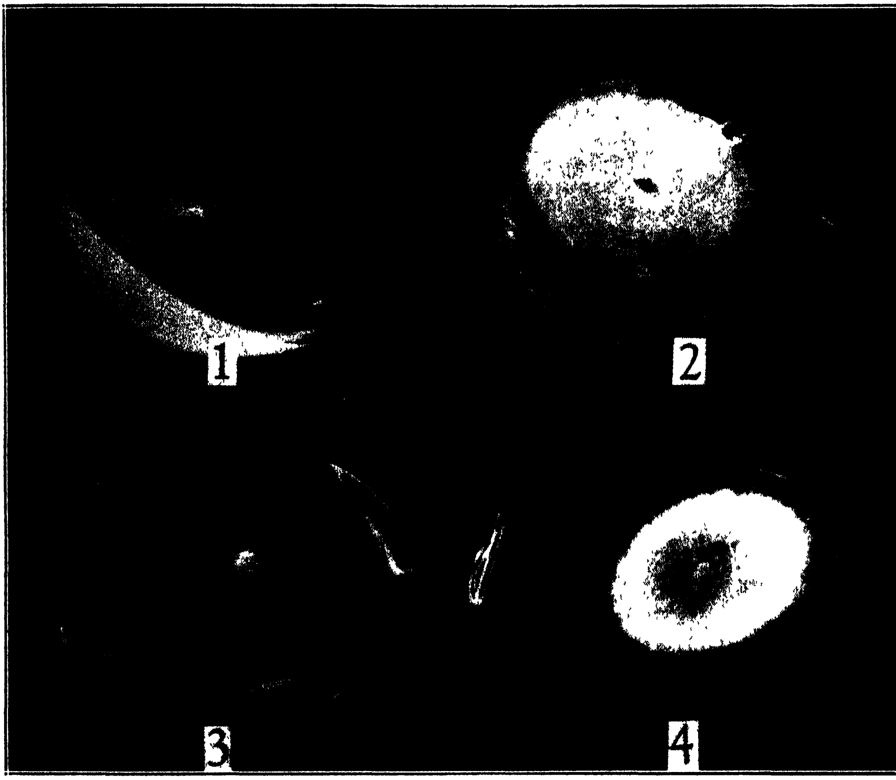


FIG. 3. Synthesis of thiazole and of thiamine by *Ceratostomella stenoceras* in a basal solution containing pyrimidine. (1) The basal solution supplemented with pyrimidine solidified with purified agar and inoculated with *Mucor ramannianus*; (2) basal solution supplemented with pyrimidine in which *C. stenoceras* was grown 11 days. After addition of agar and autoclaving inoculated with *M. ramannianus*; (3) same as (1) but inoculated with *Ceratostomella* from London plane tree (*CLP*); (4) same as (2) but inoculated with *CLP*. Age of cultures, 11 days.

DISCUSSION

Two of the organisms included in this report were previously studied. Schopfer and Blumer (10) found *Polyporus* (*Polystictus*) *versicolor* responded to a mixture of pyrimidine and thiazole, but not to one alone. Schopfer (4, 5) and Müller and Schopfer (3) found thiazole permitted growth of *M. ramannianus*; but pyrimidine was ineffective, and Schopfer

(8) reported that thiamine was formed by this fungus in a medium supplemented with thiazole only.

Combining the results obtained in this study, and those summarized by Robbins and Kavanagh (17), 19 filamentous fungi are now known which require thiamine as such (the majority of these are species of *Phytophthora*) ; 15, able to use the two intermediates; 30, which grow when supplied with pyrimidine alone. *M. ramannianus* remains as the unique example of a fungus which grows in a medium supplemented with thiazole only. We cannot explain why among thiamine-deficient fungi the ability to synthesize thiazole is so much more common than ability to synthesize pyrimidine. If we consider that thiamine-deficient fungi evolved from forms autotrophic for thiamine by a progressive loss in synthetic power, the course of events would appear to have been as follows: loss of ability to make one of the thiamine intermediates followed by loss of power to combine the intermediates into thiamine; and in such a sequence loss of ability to make pyrimidine would appear to have been far more frequent than to make thiazole.

Our results together with those obtained by others support the assumption that the bio-synthesis of thiamine occurs through the formation of pyrimidine and thiazole, and the combination of these intermediates into thiamine. If these processes are enzymatic, as is likely, it would seem that separate enzyme systems are concerned in the formation of thiazole, of pyrimidine, and in the union of the two to form thiamine. Otherwise it would be difficult to understand how the loss of ability to synthesize one of the intermediates could occur without at the same time causing loss of ability to synthesize another.

Are there fungi able to synthesize one or both intermediates but unable to combine them into thiamine? The existence of such organisms would be possible if independent enzyme systems are concerned in the synthesis of the intermediates and of thiamine, as suggested above, though the evolutionary sequence discussed previously would militate against their occurrence. If such fungi exist, and this is not probable, they would be included in the group which requires the addition of molecular thiamine to the medium, and they could be identified by the proper bioassays under conditions in which the amount of thiazole and pyrimidine in the original cultures was known.

In any event, the results of these investigations emphasize the importance of thiamine as an essential metabolite for the fungi.

THE NEW YORK BOTANICAL GARDEN
AND
DEPARTMENT OF BOTANY, COLUMBIA UNIVERSITY

Literature Cited

1. **Beadle, G. W. & Tatum, E. L.** Genetic control of biochemical reactions in *Neurospora*. Proc. Nat. Acad. 27: 499–506. 1941.

2. **Bonner, J. & Buchman, E. R.** The synthesis and destruction of vitamin B_1 by *Phycomyces*. Proc. Nat. Acad. **25**: 164–171. 1939.
3. **Müller, W. & Schopfer, W. H.** L'action de l'aneurine et de ses constituants sur *Mucor Ramannianus* Möll. Compt. Rend. Acad. Sci. Paris **205**: 687–689. 1937.
4. **Schopfer, W. H.** Études sur les facteurs de croissance. Sur la multiplicité des facteurs agissant sur les Mucorinées. Bull. Soc. Bot. Suisse **43**: 389–404. 1934.
5. **Schopfer, W. H.** Étude sur les facteurs de croissance. Action de la vitamine cristalisée B_1 et de l'extrait de germe de blé sur *Rhizopus* et d'autres Mucorinées. Zeits. Vitaminforsch. **4**: 187–206. 1935.
6. **Schopfer, W. H.** L'action des constituants de l'aneurine sur des levures (*Rhodotorula rubra* et *flava*). Compt. Rend. Acad. Sci. Paris **205**: 445–447. 1937.
7. **Schopfer, W. H.** La pyrimidine (2-methyl-4 amino-5-amino-methyl-pyrimidine), facteur de croissance de microorganisme (*Rhodotorula*, Mucorinées, *Dematium*). Protoplasma **31**: 105–135. 1938.
8. **Schopfer, W. H.** Le problème du métabolisme de l'aneurine chez les plantes. 12 p. Berne. 1940.
9. **Schopfer, W. H. & Blumer, S.** Le pouvoir de synthèse d'un facteur de croissance par *Schizophyllum commune* (haplontes et diplonte). Protoplasma **34**: 524–532. 1940.
10. **Schopfer, W. H. & Blumer, S.** Recherches sur la repartition de l'hétérotrophie par rapport a l'aneurine chez les champignons. Arch. Mikrobiol. **11**: 205–214. 1940.
11. **Schopfer, W. H. & Jung, A.** Recherches sur la synthèse de la vitamine B_1 par *Phycomyces*. Arch. Mikrobiol. **6**: 345–349. 1935.
12. **Schopfer, W. H. & Jung, A.** L'action des produits de désintégration de l'aneurine sur *Phycomyces*. Le second facteur de croissance des Mucorinées. Compt. Rend. Acad. Sci. Paris **204**: 1500–1502. 1937.
13. **Robbins, William J.** Organisms requiring vitamin B_1. Proc. Nat. Acad. **24**: 53–56. 1938.
14. **Robbins, William J.** Thiamin and growth of species of *Phytophthora*. Bull. Torrey Club **65**: 267–276. 1938.
15. **Robbins, William J.** Thiamin and plant growth. Science **89**: 303–307. 1939.
16. **Robbins, W. J. & Kavanagh, F.** Intermediates of vitamin B_1 and growth of *Phycomyces*. Proc. Nat. Acad. **23**: 499–502. 1937.
17. **Robbins, W. J. & Kavanagh, Virgene.** Vitamin deficiencies of the filamentous fungi. Bot. Rev. **8**: 411–471. 1942.
18. **Robbins, W. J. & Ma, Roberta.** Vitamin deficiencies of *Ceratostomella*. Bull. Torrey Club **69**: 184–203. 1942.
19. **Robbins, W. J. & Ma, Roberta.** Vitamin deficiencies of twelve fungi. Arch. Biochem. **1**: 219–229. 1942.
20. **Robbins, W. J. & Ma, Roberta.** Vitamin deficiencies of *Ceratostomella* and related fungi. Am. Jour. Bot. **29**: 835–843. 1942.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

The Index to American Botanical Literature is classified under 8 headings as follows: Plant Taxonomy and Floristics (exclusive of fungi); Morphology (including anatomy, and cytology in part); Plant Physiology; Mycology and Phytopathology; Genetics (including cytogenetics); Paleobotany; Ecology and Plant Geography; General Botany (including biography). It is realized that some articles do not fall readily in any of these classifications, and users of the Index interested in a particular topic are requested to examine also classifications which may include closely related topics.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)

Alexander, E. J. *Anthericum Chandleri.* Lila de los llanos. Native of southern Texas and Mexico. Addisonia **21:** 49, 50. *pl. 697.* 30 N 1942 [7 Ja 1943].

Alexander, E. J. *Commelinantia anomala.* Addisonia **21:** 55, 56. *pl. 700.* 31 N 1942 [7 Ja 1943].

Alexander, E. J. *Grindelia oolepis.* Native of southern Texas. Addisonia **21:** 63, 64. *pl. 704.* 30 N 1942 [7 Ja 1943].

Alexander, E. J. *Renealmia ventricosa.* Native of Cuba. Addisonia **21:** 51. *pl. 698.* 30 N 1942 [7 Ja 1943].

Alexander, E. J. *Talinum Mengesii.* Native of southeastern United States. Addisonia **21:** 61, 62. *pl. 703.* 30 N 1942 [7 Ja 1943].

Alexander, E. J. *Tradescantia micrantha.* Native of southern Texas and adjacent Mexico. Addisonia **21:** 53, 54. *pl. 699.* 30 N 1942 [7 Ja 1943].

Alexander, E. J. *Trixis radialis.* Native of tropical America. Addisonia **21:** 57. *pl. 701.* 30 N 1942 [7 Ja 1943].

Ames, O. & Correll, D. S. Notes on American orchids. Bot. Mus. Leafl. **11:** 1–28. *pl. 1–3.* 22 Ja 1943.

Andrews, A. L. Taxonomic notes. II. Another natural hybrid in the Funariaceae. Bryologist **45:** 176–178. D 1942.

Ball, C. R. *Salix Floridana* Chapman, a valid species. Jour. Arnold Arb. **24:** 103–106. *pl. 1.* Ja 1943.

Barneby, R. C. A new species of *Mirabilis*, with remarks on *Hermidium* and related genera. Leafl. West. Bot. **3:** 175–179. 19 N 1942.

Barros, M. Notas ciperológicas II. Darwiniana **6:** 122–126. *f. 1.* 15 S 1942.

Bartram, E. B. Third Archbold expedition, mosses from the Snow Mountains, Netherlands New Guinea. Lloydia **5:** 245–292. D 1942.

Blake, S. F. State floras of the United States. Chron. Bot. **7:** 258–261. D 1942.

Bomhard, M. L. *Ceroxylon ferrugineum* André, the Salento waxpalm. Jour. Wash. Acad. **33:** 1–8. *f. 1.* 15 Ja 1943.

Borsini, O. E. Polemoniaceas Argentinas. Lilloa **8:** 199–230. *f. 1–8.* 25 Jl 1942.

Brade, A. C. A composição da flora pteridófita do Itatiaia. Contribuição para a fitogeografia dessa região. Rodriguesia 6^{15}: 29–43. *pl. 1–9.* 15 Je 1942.

Bremekamp, C. E. B. Controversial questions in taxonomy. Chron. Bot. **7:** 255–258. D 1942.

Brinker, R. R. Monograph of *Schoenocaulon*. Ann. Mo. Bot. Gard. **29:** 287–314. *pl. 27–29.* 18 D 1942.

Buell, M. F. & Cain, R. L. A key to woody plants, based upon the flora of Itasca Park, Minnesota. 1–30. Lithoprinted. Burgess Pub. Co., Minn. Mr 1940.

Burkart, A. Algunas Leguminosas nuevas de la Flora Argentina. Darwiniana **4:** 323–331. *f. 1.* 22 Je 1942.

Burkart, A. Las especies de *Indigofera* de la flora Argentina. Darwiniana **4:** 145–178. *f. 1–5.* 22 Je 1942.

Burkart, A. Las Orobancáceas, especialmente *Orobanche Chilensis* y su distribución geográfica en la República Argentina. Darwiniana **4:** 303–310. *f. 1, 2.* 22 Je 1942.

Burkart, A. Nuevas contribuciones a la sistemática de las especies sudamericanas de *Lathyrus*. Darwiniana **6:** 9–30. 15 S 1942.

Butters, F. K. & Abbe, E. C. A new oxytrope of the Minnesota-Ontario border. Rhodora **45:** 1–4. *pl. 745.* Ja 1943.

Chase, A. Papuan grasses collected by L. J. Brass, III. Jour. Arnold Arb. **24:** 77–89. *f. 1–4.* Ja 1943.

Cheadle, V. I. The role of anatomy in phylogenetic studies of the Monocotyledoneae. Chron. Bot. **7:** 253, 254. D 1942.

Clark, J. H. & Gilbert, S. G. Selection of criterion leaves for the identification of blueberry varieties. Proc. Am. Soc. Hort. Sci. **40:** 347–351. My 1942.

Croizat, L. Notes on American Euphorbiaceae, with descriptions of eleven new species. Jour. Wash. Acad. **33:** 11–20. 15 Ja 1943.

Cutak, L. A new species from the Big Ben region of Texas. Cactus & Succ. Jour. **14:** 163–164. *f. 96.* D 1942.

Croizat, L. What is a cephalium? Cactus & Succ. Jour. **14:** 169–172. *f. 100.* D 1942.

Descole, H. E. Calceolarias de Tucuman (Scrophulariaceae). Lilloa **8:** 335–352. *pl. 1–8 + f. 1–3.* 25 Jl 1942.

Dore, W. G. & Roland, A. E. The grasses of Nova Scotia. Proc. Nova Scotian Inst. **20:** 177–288. *illust.* 30 D 1942.

Dwyer, J. D. *Kaieteuria*, a new genus of the Ochnaceae. Bull. Torrey Club **70:** 50–52. 2 Ja 1943.

Dwyer, J. D. The taxonomy of the monogeneric tribe Elvasieae (Ochnaceae). Bull. Torrey Club **70:** 42–49. 2 Ja 1943.

Eastwood, A. New species and varieties of *Lupinus*. Leafl. West. Bot. **3:** 169–175. 19 N 1942.

Eastwood, A. *Solanum lanceolatum* in California. Leafl. West Bot. **3:** 189, 190. 19 N 1942.

Fernald, M. L. The seventh century of additions to the flora of Virginia.

Rhodora **44:** 341–405. *pl. 717–726.* 17 O 1942, 416–452. *pl. 727–735.* 7 N 1942, 457–478. *pl. 737–744.* 26 D 1942.

Fernald, M. L. Transfers in *Scirpus* § *Actaeogeton.* Rhodora **44:** 479–484. 26 D 1942.

Filho, M. A nova sistemática. Rodriguesia 6^{15}: 45–52. 15 Je 1942.

Foster, A. S. & San Pedro, M. R. Field studies on *Microcycas calocoma.* Mem. Soc. Club. Hist. Nat. **16:** 105–121. *pl. 10–17.* 15 Au 1942.

Fraser, W. P. Notes on the willows of Saskatchewan. Canad. Field Nat. **66:** 104–110. O 1942 [7 Ja 1943].

Fulford, M. Studies on American Hepaticae IV—A revision of the genus *Symbiezidium.* Lloydia **5:** 293–304. *f. 1–14.* D 1942.

Gates, F. C. Kansas botanical notes, 1941. Trans. Kansas Acad. **45:** 92, 93. 1942.

Gilly, C. Two new species of Caryocaraceae from northern South America. Trop. Woods **72:** 16–18. 1 D 1942.

Gleason, H. A. *Scirpus koilolepis,* comb. nov. Rhodora **44:** 479. 26 D 1942.

Gould, F. W. A systematic treatment of the genus *Camassia* Lindl. Am. Midl. Nat. **28:** 712–742. *f. 1–10.* N 1942 [10 Ja 1943].

Graustein, J. E. *Penstemon laevigatus* a misnomer. Rhodora **44:** 485. 26 D 1942.

Green, G. R. Trees of North America (exclusive of Mexico). Vol. I—The Conifers pp. 1–186; Vol. II—The Broadleaves i–xvii, 1–344. lithoprinted Edwards Brothers. Ann. Arbor, Michigan. 1938.

Grondona, E. M. Las especies del género *Polygala* en la provincia de Buenos Aires. Darwiniana **6:** 83–121. *f. 1–16.* 15 S 1942.

Gruber, C. L. Additional ferns in the Kutztown-Fleetwood area, Pa. Am. Fern Jour. **32:** 151–152. O–D 1942 [13 Ja 1943].

Haupt, A. W. Studies in Californian Hepaticae III. *Cryptomitrium tenerum.* Bot. Gaz. **104:** 264–272. *f. 1–28.* 8 Ja 1943.

Herre, A. W. C. T. Additions to and comments upon the lichen flora of the Santa Cruz peninsula, California. Am. Midl. Nat. **28:** 752–755. N 1942 [10 Ja 1943].

Herre, A. W. C. T. Some noteworthy lichens from Florida. Bryologist **45:** 180. D 1942.

Higinbotham, N. *Cephalomonas,* a new genus of the Volvocales. Bull. Torrey Club **69:** 661–668. *f. 1–43.* 2 D 1942.

Holdridge, L. E. Trees of Puerto Rico, II. U. S. Dept. Agric. Trop. Forest Exp. Sta. Occ. Pap. **2:** 1–105. *illust.* S 1942.

Hollenberg, G. J. An account of the species of *Polysiphonia* on the Pacific Coast of North America. I. *Oligosiphonia.* Am. Jour. Bot. **29:** 772–785. *f. 1–12.* 13 D 1942.

Holmgren, A. H. Handbook of the vascular plants of northeastern Nevada. i–v, 1–214. mimeographed. Utah Agr. Coll. & U. S. Dept. Interior Grazing Service. 1942.

House, H. D. A few mosses collected in the Allegany State Park, Cattaraugus County, N. Y. Sci. Stud. St. Bonaventure Coll. 11^2: 3. Ja 1943.

Howell, J. T. Another bindweed in California. Leafl. West. Bot. **3:** 179. 19 N 1942.

Howell, J. T. A notable accession to the Californian chickweeds. Leafl. West. Bot. **3:** 192. 19 N 1942.

Howell, J. T. Studies in *Phacelia*—III. Leafl. West. Bot. **3:** 190–192. 19 N 1942.

Howell, J. T. A short list of plants from Cedros Island, Lower California. Leafl. West. Bot. **3:** 181–185. 19 N 1942.

Howell, J. T. Western plants from here and there. Leafl. West Bot. **3:** 187–188. 19 N 1942.

Hunt, K. W. Ferns of the vicinity of Charleston, S. C. Charleston Mus. Leafl. **17:** 1–5. D 1942.

Hyland, F. New combinations in *Pyrus*. Rhodora **45:** 28. Ja 1943.

Johnston, I. M. New Phanerogams from Mexico, V. Jour. Arnold Arb. **24:** 90–98. Ja 1943.

Kobuski, C. E. Studies in the Theaceae, XIV. Notes on the West Indian species of *Ternstroemia*. Jour. Arnold Arb. **24:** 60–76. Ja 1943.

Knobloch, I. W. A fern collection from Chihuahua. Am. Fern Jour. **32:** 127–138. O–D 1942. [13 Ja 1943].

Kuhlmann, J. G. A floração da *Dialypetalanthus fuscescens*, Kuhlman, no Jardim Botânico. Rodriguesia **6**[15]: 27. *1 pl.* 15 Je 1942.

Kuhlmann, J. G. Rubiaceae *Dialypetalanthus* Kuhlmann. Rodriguesia **6**[15]: 25, 26. *1 pl.* 15 Je 1942.

Lawrence, G. H. M. & Schulze, A. E. The cultivated *Hederae*. Gentes Herb. **6:** 107–173. *f. 74–86.* 27 N 1942.

Leonard, E. C. Three new species of Acanthaceae from Mexico. Jour. Wash. Acad. **32:** 341–343. 15 N 1942.

Li, Hui-Lin. *Schizomussaenda*, a new genus of the Rubiaceae. Jour. Arnold Arb. **24:** 99–102. Ja 1943.

Little, E. L. New names in *Quercus* and *Osmanthus*. Jour. Wash. Acad. **33:** 8–11. 15 Ja 1943.

Lourteig, A. Primulaceae Argentinae Lilloa **8:** 231–267. *pl. 1* + *f. 1–9.* 25 Jl 1942.

Lourteig, A. & O'Donell, C. A. Acalypheae Argentinae (Euphorbiaceae). Lilloa **8:** 273–333. *pl. 1–9* + *f. 1–19.* 25 Jl 1942.

McFarland, F. T. A catalogue of the vascular plants of Kentucky. Castanea **7:** 77–108. O–D 1942.

Machado, O. Contribuição ao estudo de *Datura insignis* Barb. Rod. Rodriguesia **6**[15]: 17–23. *pl. 1–4.* 15 Je 1942.

McVaugh, R. Campanulales: Campanulaceae, Lobelioideae. North American Flora **32A:** 1–134. 5 Ja 1943

Marie-Victorin, *Frère*. *Dracaena cubensis*. Une relique d'affinité Africaine dans la flora de Cuba. Contr. Inst. Bot. Univ. Montreal **43:** 1–16. *f. 1–10.* 1942.

Marie-Victorin, *Frère* & Rolland-Germain, *Frère*. Premières observations botaniques sur la nouvelle route de l'Abitibi (Mont-Laurier-Senneterre). Contr. Inst. Bot. Univ. Montreal **42:** 1–48. *f. 1–22.* 1942.

Martinez, M. Una nueve Pináceae Mexicana. *Pinus durangensis* sp. nov. An. Inst. Biol. Mexico **13:** 23–29. *f. 1–4.* 1942. *Picea chihuahuana* sp. nov. 31–34. *f. 1–4.* Una Rubiaceae nueva de Mexico. 35–41. *f. 1–4.*

Mathias, M. E. & Constance, L. New North American Umbelliferae—II. Bull. Torrey Club **70:** 58–60. 2 Ja 1943.

Mendoza, E. Las especies de *Asparagus* cultivadas en la Argentina. Darwiniana **4:** 311–323. 22 Je 1942.

Merrill, E. D. & Perry, L. M. Plantae Papuanae Archboldiana, X. Jour. Arnold Arb. **23:** 383–416. O 1942. XI. **24:** 34–59. *f. 1–7.* Ja 1943.

Meyer, T. Revision de las especies Argentinas del genero *Mitostigma* (Asclepiadaceae). Lilloa **8:** 1–36. *pl. 1–7* + *f. 1–2.* 25 Jl 1942.

Miranda, F. Estudios sobre la vegetación de Mexico. II. Observaciones preliminares sobre la vegetacion de la region de Tapachula, Chiapas (1). An. Inst. Biol. Mexico **13:** 53–70. *f. 1–17.* 1942.

Moldenke, H. N. *Verbena maritima.* Beach Vervain. Native of Florida. Addisonia **21:** 59, 60. *pl. 702.* 30 N 1942. [7 Ja 1943].

Moran, R. The generic status of *Hasseanthus.* Desert **14:** 165–169. *f. 1–3.* N 1942.

Moran, R. The status of *Dudleya* and *Stylophyllum.* Desert **14:** 149–157. *f. 1, 2.* O 1942.

Moyle, J. B. A field key to the common non-woody flowering plants and ferns of Minnesota. rev. ed. 1–71. lithoprinted. Burgess Pub. Co., Minneapolis, Minn. 1941.

Muenscher, W. C. & Winne, W. T. Common poisonous plants. Cornell Ext. Bull. 538: 1–31. *f. 1–20.* S 1942.

Muller, C. H. A new species of *Quercus* in Texas. Am. Midl. Nat. **28:** 743–745. *f. 1.* N 1942 [10 Ja 1943].

Munz, P. A. Studies in Onagraceae XII. A revision of the New World species of *Jussiaea.* Darwiniana **4:** 179–284. *pl. 1–20* + *f. 1–10.* 22 Je 1942.

O'Donell, C. A. & Lourteig, A. Chrozophoreae Argentinae. Lilloa **8:** 37–81. *f. 1–10.* 25 Jl 1942.

Olmo, H. P. The use of seed characters in the identification of grape varieties. Proc. Am. Soc. Hort. Sci. **40:** 305–309. My 1942.

Pierce, J. H. The American species of *Daubentonia* (Leguminosae). Trop. Woods **72:** 12–15. 1 D 1942.

Porsild, A. E. Miscellaneous contributions from the National Herbarium of Canada, III. Canad. Field Nat. **66:** 112, 113. O 1942 [7 Ja 1943].

Ragonese, A. E. & Covas, G. Flora de la Provincia de Santa Fé (Rep. Argentina). Las Palmeras. Darwiniana **4:** 285–302. *pl. 1–3* + *f. 1–5.* 22 Je 1942.

Record, S. J. American timbers of the genera *Dalbergia* and *Machaerium.* Trop. Woods **72:** 1–11. 1 D 1942.

Record, S. J. Keys to American woods. Trop. Woods **72:** 19–35. 1 D 1942.

Reeder, J. R. The status of *Distichlis dentata.* Bull. Torrey Club **70:** 53–57. *f. 1.* 2 Ja 1943.

Reeves, R. G. & Mangelsdorf, P. C. A proposed taxonomic change in the tribe Maydeae (family Gramineae). Am. Jour. Bot. **29:** 815–817. D 1942 [18 Ja 1943].

St. John, E. P. A new *Thelypteris* from Florida. Am. Fern Jour. **32:** 145–147. O–D 1942 [13 Ja 1943].

Scanlon, G. M. A study of the genus *Cyperus* in the Hawaiian Islands. Catholic Univ. Am. Biol. Ser. **41:** 1–62. 1942.

Schulz, A. G. Las Pontederiáceas de la Argentina. Darwiniana **6:** 45–82. *pl. 1–5* + *f. 1–13.* 15 S 1942.

Shanks, R. E. The vegetation of Trumbull County, Ohio. Ohio Jour. Sci. **42:** 220–236. N 1942.

Shaver, J. M. Some general notes on ferns. Jour. Tenn. Acad. **17:** 311–336. *pl. 1* + *f. 1–7.* O 1942.

Sherff, E. E. Revision of the Hawaiian members of the genus *Pittosporum* Banks. Field Mus. Bot. Ser. **22**[10]: 467–566. 16 N 1942.

Sherff, E. E. Some new or otherwise noteworthy Mexican Coreopsideae (Genera *Heterosperma* Cav. and *Bidens* L.) and a note on *Xylosma Hawaiiense* Seem. Field Mus. Bot. Ser. **22**[10]: 567–573. 10 N 1942.

Smith, A. C. The American species of *Drimys*. Jour. Arnold Arb. **24:** 1–33. *f. 1–3*. Ja 1943.

Standley, P. C. & Steyermark, J. A. Studies of Central American plants—III. Field Mus. Bot. Ser. **23**[1]: 1–28. 14 Ja 1943.

Stebbins, G. L. The concept of genetic homogeneity as an explanation for the existence and behavior of rare and endemic species. Chron. Bot. **7:** 252, 253. D 1942.

Steere, W. C. Notes on Michigan Bryophytes—VI. Bryologist **45:** 153–172. D 1942.

Stehlé, H. Catalogue des cryptogames vasculaires des Antilles Francaises. Carib. Forester **4:** 35–47. O 1942.

Stevens, W. C. & Dill, F. E. *Aplectrum spicatum* in a Kansas woodland. Trans. Kansas Acad. **45:** 138–144. *pl. 1–4*. 1942.

Taft, C. E. Additions to the algae of the west end of Lake Erie. Ohio Jour. Sci. **42:** 251–256. *pl. 1, 2*. N 1942.

Taylor, W. R. Caribbean marine algae of the Allan Hancock Expedition, 1939. Allan Hancock Atlantic Exped. Rep. **2:** 1–193. *pl. 1–20*. N–D 1942.

Thorpe, H. G. *Alchemilla pratensis* in Erie County, New York. Rhodora **45:** 27. Ja 1943.

Turrill, W. B. Taxonomy and phylogeny. Bot. Rev. **8:** 655–707. D 1942.

Upham, A. W. *Epipactis latifolia* in New Hampshire. Rhodora **44:** 456, 457. 26 D 1942.

Vassilchenko, I. I. Über die Bedeutung der Keimungsmorphologie für die phylogenetische Systematik der Blütenpflanzen. Chron. Bot. **7:** 254, 255. D 1942.

Wheeler, L. C. *Amaranthus Powellii* in California. Leafl. West. Bot. **3:** 185–187. 19 N 1942.

Wherry, E. T. The discoveries of new Pennsylvania ferns. Am. Fern Jour. **32:** 148, 149. O–D 1942 [13 Ja 1943].

Wherry, E. T. Observations on Florida ferns. Am. Fern Jour. **32:** 139–145. O–D 1942 [13 Ja 1943].

Wherry, E. T. The Phloxes of Nevada. Not. Nat. **113:** 1–11. 20 N 1942.

Wherry, E. T. Relationship of *Lilium Michiganense*. Rhodora **44:** 453–456. 26 D 1942.

Wiggins, I. L. New locality for a curious California polypody. Am. Fern Jour. **32:** 149–151. *pl. 12*. O–D 1942 [13 Ja 1943].

Williams, L. O. A new *Epidendrum* from Panama. Am. Orchid Soc. Bull. **11:** 249. *pl. 7*. 1 D 1942.

Williams, L. O. Two new Saccoglossums from New Guinea. Am. Orchid Soc. Bull. **11:** 297–299. *pl. 8*. 7 Ja 1943.

Woodson, R. E. & Schery, R. W. Contributions toward a flora of Panama. VI. Collections chiefly by H. von Wedel in Bocas del Toro. Ann. Mo. Bot. Gard. **29:** 317–378. *pl. 30–34* + *1 f*. 18 D 1942.

Yuncker, T. G. Nomenclatural changes in the genus *Cuscuta*, and notes on some American species. Bull. Torrey Club **70:** 61–67. 2 Ja 1943.

MORPHOLOGY

(including anatomy, and cytology in part)
(See also under Taxonomy. **Cheadle, Vassilchenko**)

Burton, G. W. Observations on the flowering habits of four *Paspalum* species. Am. Jour. Bot. **29:** 843–848. *f. 1–3*. D 1942 [18 Ja 1943].

Esau, K. Vascular differentiation in the vegetative shoot of *Linum*. I. The procambium. Am. Jour. Bot. **29**: 738–747. *f. 1–29.* 13 D 1942. [18 Ja 1943].

Ford, E. S. Anatomy and histology of the Eureka lemon. Bot. Gaz. **104**: 288–305. *f. 1–47.* 8 Ja 1943.

Fulford, M. Development of sporelings in the Lejeuneaceae. Bull. Torrey Club **69**: 627–633. 2 D 1942.

Fulford, M. Sporelings and vegetative reproductive structures in *Archilejeunea*. Bryologist **45**: 173–175. *f. 1–20.* D 1942.

Fulford, M. Sporelings and vegetative reproductive structures in *Mastigolejeunea auriculata*. Am. Jour. Bot. **29**: 848–850. *f. 1–19.* D 1942. [18 Ja 1943]

Gier, L. J. & Burress, R. M. Anatomy of *Taraxacum officinale* 'Weber.' Trans. Kansas Acad. **45**: 94–97. *f. A–E.* 1942.

Gifford, E. M. The structure and development of the shoot apex of *Ephedra altissima* Desf. Bull. Torrey Club **70**: 15–25. *f. 1–11.* 2 Ja 1943.

Goodwin, R. H. On the development of xylary elements in the first internode of *Avena* in dark and light. Am. Jour. Bot. **29**: 818–828. D 1942. [18 Ja 1943].

Hartzell, A. Vegetative propagation of red squill. Contr. Boyce Thompson Inst. **12**: 481–483. *f. 1.* 15 D 1942.

Heimsch, C. Comparative anatomy of the secondary xylem in the *Gruinales* and *Terebinthales* of Wettstein with reference to taxonomic grouping. Lilloa **8**: 85–198. *pl. 1–17.* 25 Jl 1942.

Higinbotham, N. The three-dimensional shapes of undifferentiated cells in the petiole of *Angiopteris evecta*. Am. Jour. Bot. **29**: 851–858. *f. 1–16.* D 1942 [18 Ja 1943].

Palser, B. F. Histological responses of *Vicia faba* to indoleacetic acid. Bot. Gaz. **104**: 243–263. *f. 1–23.* 8 Ja 1943.

Reeve, R. M. Structure and growth of the vegetative shoot apex of *Garrya elliptica* Dougl. Am. Jour. Bot. **29**: 697–710. *pl. 1–5.* 13 D 1942.

Simonds, A. O. Histological study of freezing, desiccation, and winter injury of raspberry canes. Bot. Gaz. **104**: 356–361. *f. 1–8.* 8 Ja 1943.

Struckmeyer, B. E. & Roberts, R. H. Investigations on the time of blossom induction in wealthy apple trees. Proc. Am. Soc. Hort. Sci. **40**: 113–119. *f. 1–4.* My 1942.

Trent, J. A. Studies pertaining to the life history of *Specularia perfoliata* (L.) A. DC., with special reference to cleistogamy. Trans. Kansas Acad. **45**: 152–164. *pl. 1–4.* 1942.

Villagran Prado, F. Contribucion al conocimiento de la histologia y citologia del Maguey (*Agave*). An. Inst. Biol. Mexico **13**: 43–46. *f. 1–4.* 1942.

Vivian, V. E. Symmetry studies in *Sagina*. Bull. Torrey Club **69**: 634–646. *f. 1–72.* 2 D 1942.

Wilson, C. L. The telome theory and the origin of the stamen. Am. Jour. Bot. **29**: 759–764. *f. 1–29.* 13 D 1942.

PLANT PHYSIOLOGY

(See also under Mycology: **Braun & Laskaris**)

Arnon, D. I., Fratzke, W. E. & Johnson, C. M. Hydrogen ion concentration in relation to absorption in inorganic nutrients by higher plants. Plant Physiol. **17**: 515–524. *f. 12.* O 1942.

Avery, G. S., Berger, J. & Shalucha, B. Auxin content of maize kernels during

ontogeny, from plants of varying heterotic vigor. Am. Jour. Bot. **29:** 765–772. *f. 1–5.* 13 D 1924.

Avery, G. S., Berger, J. & Shalucha, B. Comparative activity of synthetic auxins and derivatives. Bot. Gaz. **104:** 281–287. 8 Ja 1943.

Ayers, A. D. Comparison of the calcium and sulphur content of plant fluids expressed from tissues killed by autoclaving and freezing with solid carbon dioxide. Plant Physiol. **17:** 661–665. O 1942.

Bair, R. A. Growth rates of maize under field conditions. Plant Physiol. **17:** 619–631. *f. 1–6.* O 1942.

Baker, D. & Nelson, J. M. Tyrosinase and plant respiration. Jour. Gen. Physiol. **26:** 269–276. 20 Ja 1943.

Burrell, A. B., Cain, J. C. & Brinkerhoff, L. A. Response of apple trees to potash in the Champlain Valley. II. A third-year growth response and a first-year reduction in leaf-scorch. Proc. Am. Soc. Hort. Sci. **40:** 8–12. My 1942.

Carroll, G. H. The rôle of ascorbic acid in plant nutrition. Bot. Rev. **9:** 41–48. Ja 1943.

Childers, N. F. & White, D. G. Influence of submersion of the roots on transpiration, apparent photosynthesis, and respiration of young apple trees. Plant Physiol. **17:** 603–618. *f. 1–9.* O 1942.

Cochran, H. L. Influence of photoperiod on the time of flower primordia differentiation in the perfection pimiento (*Capsicum frutescens* L.). Proc. Am. Soc. Hort. Sci. **40:** 493–497. *f. 1.* My 1942.

Colwell, R. N. The use of radioactive phosphorus in translocation studies. Am. Jour. Bot. **29:** 798–807. *f. 1–9.* D 1942 [18 Ja 1943].

Commoner, B. & Mazia, D. The mechanism of auxin action. Plant Physiol. **17:** 682–685. *f. 1.* O 1942.

Davis, L. D. The relation between diameter and fresh weight of developing peach fruits Proc. Am. Soc. Hort. Sci. **40:** 146–152. My 1942.

Dawson, R. F. Nicotine synthesis in excised tobacco roots. Am. Jour. Bot. **29:** 813–815. D 1942 [18 Ja 1943].

Denny, F. E. Effect of a few hours of chilling upon the germination of gladiolus corms subjected to an artificially prolonged rest period. Contr. Boyce Thompson Inst. **12:** 375–386. *f. 1, 2.* Jl–S 1942.

Denny, F. E. The use of methyl ester of α naphthaleneacetic acid for inhibiting sprouting of potato tubers, and an estimate of the amount of chemical retained by tubers. Contr. Boyce Thompson Inst. **12:** 387–403. *f. 1–4.* Jl–S 1942.

Denny, F. E. & Thornton, N. C. The third year's results on storage of potato tubers in relation to sugar content and color of potato chips. Contr. Boyce Thompson Inst. **12:** 405–429. *f. 1, 2.* Jl–S 1942.

Eaton, S. V. Influence of sulphur deficiency on metabolism of black mustard. Bot. Gaz. **104:** 306–315. *f. 1.* 8 Ja 1943.

Eyster, H. C. Enzymes and the law of mass action. Plant Physiol. **17:** 686–688. O 1942.

Flemion, F. Effect of the addition of nitrogen upon germination of seeds of *Symphoricarpos racemosus.* Contr. Boyce Thompson Inst. **12:** 485–489. 15 D 1942.

Flint, L. H. & Moreland, C. F. A comparison of the effects of green light and red light on the simple-leaf development of intact and decapitated bean plants. Plant Physiol. **17:** 677–681. *f. 1.* O 1942.

Gustafson, F. G. β-Naphthoxyacetic acid as an inductor of parthenocarpy in tomatoes. Proc. Am. Soc. Hort. Sci. **40**: 387–389. My 1942.

Harvey, E. N. Hydrostatic pressure and temperature in relation to stimulation and cyclosis in *Nitella flexilis*. Jour. Gen. Physiol. **25**: 855–863. 20 Jl 1942.

Hitchcock, A. E. & Zimmerman, P. W. Root-inducing substances effective on apple cuttings taken in May. Proc. Am. Soc. Hort. Sci. **40**: 292–297. *f. 1–2.* My 1942.

Hitchcock, A. E. & Zimmerman, P. W. Root-inducing activity of phenoxy compounds in relation to their structure. Contr. Boyce Thompson Inst. **12**: 497–507. *f. 1–4.* 15 D 1942.

Hoagland, D. R. & Broyer, T. C. Accumulation of salt and permeability in plant cells. Jour. Gen. Physiol. **25**: 865–880. 25 Jl 1942.

Hodgkiss, W. S. *et al.* The amount of boron absorbed by soybean plants and its effect on their growth. Plant Physiol. **17**: 652–660. *f. 1.* O 1942.

Janes, B. E. A comparison of the chemical composition of artificially produced parthenocarpic fruits and normal seeded fruits of peppers. Proc. Am. Soc. Hort. Sci. **40**: 432–436. *f. 1–2.* My 1942.

Kavanagh, F. The interaction between thiamine and four fungi. Bull. Torrey Club **69**: 669–692. *f. 1–16.* 2 D 1942.

Kienholz, J. R. Boron deficiency in pear tree. Phytopathology **32**: 1082. *f. 1.* D 1942.

Kramer, P. J. Species differences with respect to water absorption at low soil temperatures. Am. Jour. Bot. **29**: 828–832. D 1942 [18 Ja 1943].

Lee, F. A. & Tukey, H. B. Chemical changes accompanying growth and development of seed and fruit of the Elberta peach. Bot. Gaz. **104**: 348–355. *f. 1.* 8 Ja 1943.

Lowenhaupt, B. Nutritional effects of boron on growth and development of the sunflower. Bot. Gaz. **104**: 316–322. 8 Ja 1943.

Lyman, C. & Dean, L. A. Zinc deficiency of pineapples in relation to soil and plant composition. Soil Science **54**: 315–324. N 1942.

McIlvanie, S. K. Carbohydrate and nitrogen trends in bluefinch wheatgrass, *Agropyron spicatum*, with special reference to grazing influences. Plant Physiol. **17**: 540–557. *f. 1–8.* O 1942.

Macht, D. I. Influence of sulfanilamide and derivatives on growth of *Lupinus albus*. Plant Physiol. **17**: 671–676. O 1942.

Miller, L. P. Synthesis of β-2-trichloroethyl-D-glucoside and its isolation from corn and dandelion plants treated with chloral hydrate. Contr. Boyce Thompson Inst. **12**: 465–470. 15 D 1942.

Mithchell, J. W. & Whitehead, M. R. Effects of vaporous naphthoxyacetic acid on development of tomato fruits with special reference to their vitamin C content. Bot. Gaz. **104**: 362–365. *f. 1–2.* 8 Ja 1943.

Mullison, W. R. & Mullison, E. Growth responses of barley seedlings in relation to potassium and sodium nutrition. Plant Physiol. **17**: 632–644. *f. 1–3.* O 1942.

Murneek, A. E. & Wittwer, S. H. Relation of sexual reproduction to development of horticultural plants. I. General effects of flower and fruit production. Proc. Am. Soc. Hort. Sci. **40**: 201–204. My 1942.

Nightingale, G. T. Potassium and phosphate nutrition of pineapple in relation to nitrate and carbohydrate reserves. Bot. Gaz. **104**: 191–223. *f. 1–25.* 8 Ja 1943.

Olson, L. C. & Bledsoe, R. P. The chemical composition of the cotton plant and the uptake of nutrients at different stages of growth. Ga. Exp. Sta. Bull. 222: 1–16. *illust.* O 1942.

Oserkowsky, J. Polar and apolar transport of *Auxin* in woody stems. Am. Jour. Bot. **29**: 858–866. D 1942 [18 Ja 1943].

Parker, M. W. & Borthwick, H. A. Day length and crop yields. U. S. Dept. Agr. Misc. Publ. 507: 1–22. *illust.* S 1942.

Pickett, B. S. Initiation of peach flower parts. Proc. Am. Soc. Hort. Sci. **40**: 111, 112. My 1942.

Raper, J. E. Sexual hormones in *Achlya* V. Hormone A[1], a male-secreted augmenter or activator of hormone A. Proc. Nat. Acad. **28**: 509–516. D 1942.

Ratajak, E. J. & Owens, H. S. Optimal conditions for the hydrolysis of arabogalactan by *Aspergillus niger*. Bot. Gaz. **104**: 329–337. 8 Ja 1943.

Reitz, L. P. Indications of hail resistance among varieties of winter wheat. Trans. Kansas Acad. **45**: 129–137. *f. 1.* 1942.

Reuther, W. & Burrows, F. W. The effect of manganese sulfate on the photosynthetic activity of frenched tung foliage. Proc. Am. Soc. Hort. Sci. **40**: 73–76. *f. 1.* My 1942.

Robbins, W. J., Kavanagh, V. W. & Kavanagh, F. Growth substances and dormancy of *Phycomyces*. Bot. Gaz. **104**: 224–242. *f. 1.* 8 Ja 1943.

Robbins, W. J. & Ma, R. Vitamin deficiencies of *Ceratostomella* and related fungi. Am. Jour. Bot. **29**: 835–843. *f. 1–3.* D 1942 [18 Ja 1943].

Rogers, H. T., Pearson, R. W. & Pierre, W. H. The source and phosphatase activity of exoenzyme systems of corn and tomato roots. Soil Science **54**: 353–366. *f. 1–8.* N 1942.

Romshe, F. A. Correlation between fresh weight and area of tomato leaves. Proc. Am. Soc. Hort. Sci. **40**: 482. My 1942.

Smith, G. F. & Kersten, H. Auxin and calines in seedlings from X-rayed seeds. Am. Jour. Bot. **29**: 785–791. *f. 1–5.* 13 D 1942.

Scott, D. H., Waugh, J. G. & Cullinan, F. P. An injurious effect of peach juice on germination of the seed. Proc. Am. Soc. Hort. Sci. **40**: 283–285. My 1942.

Somers, I. I. & Shive, J. W. The iron manganese relation to plant metabolism. Plant Physiol. **17**: 582–602. *f. 1–6.* O 1942.

Stewart, W. S. & Hamner, C. L. Treatment of seeds with synthetic growth-regulating substances. Bot. Gaz. **104**: 338–347. *f. 1–2.* 8 Ja 1943.

Sweeney, B. M. The effect of colamine on growth and protoplasmic streaming in *Avena*. Am. Jour. Bot. **29**: 793–797. *f. 1–7.* D 1942 [18 Ja 1943].

Sweeney, B. M. & Thimann, K. V. The effect of auxins on protoplasmic streaming. III. Jour. Gen. Physiol. **25**: 841–854. 20 Jl 1942.

Taylor, D. L. Influence of oxygen tension on respiration, fermentation, and growth in wheat and rice. Am. Jour. Bot. **29**: 721–738. *f. 1–7.* 13 D 1942.

Turrell, F. M. & Fisher, P. L. The proximate chemical constituents of *Citrus* woods, with special reference to lignin. Plant Physiol. **17**: 558–581. *f. 1–3.* O 1942.

Van Fleet, D. S. The significance of oxidation in the endodermis. Am. Jour. Bot. **29**: 747–755. *f. 1–8.* 13 D 1942.

Vinson C. G. & Cross, F. B. Vitamin C content of persimmon leaves and fruits. Science **96**: 430, 431. 6 N 1942.

Wall, R. F. & Hartman, E. L. Sand culture studies of the effects of various

concentrations of added salts upon the composition of tomato plants. Proc. Am. Soc. Hort. Sci. **40:** 460–466. *f. 1–5.* My 1942.

Warne, I. G. G. The supply of water to transpiring leaves. Am. Jour. Bot. **29:** 875–884. D 1942 [18 Ja 1943].

Zimmerman, P. W. & Hitchcock, A. E. Flowering habit and correlation organs modified by triiodobenzoic acid. Contr. Boyce Thompson Inst. **12:** 491–496. *f. 1–3.* 15 D 1942.

GENETICS
(including cytogenetics)
(See also under Taxonomy: Stebbins)

Bailey, J. S. & French, A. P. The inheritance of blossom type and blossom size in the peach. Proc. Am. Soc. Hort. Sci. **40:** 248–250. My 1942.

Baldwin, J. T. Polyploidy in *Sedum pulchellum*—I. Cytogeography. Bull. Torrey Club **70:** 26–33. *f. 1–10.* 2 Ja 1943.

Charles, D. R. & Goodwin, R. H. An estimate of the minimum number of genes differentiating two species of golden-rod with respect to their morphological characters. Am. Nat. **77:** 53–69. *f. 1, 2.* Ja–F 1943.

French, A. P. & Southwick, L. Further observations on a narrow leaf variation of the apple. Proc. Am. Soc. Hort. Sci. **40:** 245–247. *f. 1–2.* My 1942.

Frost, H. B. & Krug, C. A. Diploid-tetraploid periclinal chimeras as bud variants in *Citrus.* Genetics **27:** 619–634. *f. 1–12.* N 1942.

Jones, H. A. Hybrid vigor studies with cucurbits and tomatoes. Chron. Bot. **7:** 265, 266. D 1942.

Jones, R. E. & Bamford, R. Chromosome number in the progeny of triploid *Gladiolus* with special reference to the contribution of the triploid. Am. Jour. Bot. **29:** 807–813. *f. 1–12.* D 1942 [18 Ja 1943].

Li, C. H., Pao, W. K. & Li, H. W. Interspecific crosses in *Setaria.* II. Cytological studies of interspecific hybrids involving: 1, *S. faberii* and *S. italica,* and 2, a three way cross, F_2 of *S. italica* × *S. viridis* and *S. faberii.* Jour. Hered. **33:** 351–355. *f. 7–9.* O 1942.

Longley, L. E. Color in two garden chrysanthemum crosses. Proc. Am. Soc. Hort. Sci. **40:** 583, 584. My 1942.

McClintock, B. The fusion of broken ends of chromosomes following nuclear fusion. Proc. Nat. Acad. **28:** 458–463. N 1942.

Marinelli, L. D. *et al.* Chromosomal effects of low X-ray doses on five day *Tradescantia* microspores. Am. Jour. Bot. **29:** 866–874. D 1942 [18 Ja 1943].

Marshak, A. & Malloch, W. S. The effect of fast neutrons on chromosomes in meiosis and its bearing upon pachytene pairing. Genetics **27:** 576–583. N 1942.

Martini, M. L. & Harlan, H. V. Barley freaks. Jour. Hered. **33:** 339–343. *f. 1–3.* O 1942.

Nichols, C. The effects of age and irradiation in chromosomal aberrations in *Allium* seed. Am. Jour. Bot. **29:** 755–759. 13 D 1942.

Powers, L. The nature of the series of environmental variances and the estimation of the genetic variances and the geometric means in crosses involving species of *Lycopersicon.* Genetics **27:** 561–575. N 1942.

Quinby, J. R. & Karper, R. E. Inheritance of mature plant characters in sorghum. Jour. Hered. **33:** 323–327. *f. 5, 6.* S 1942.

Reece, P. C. Differentiation of avocado blossom buds in Florida. Bot. Gaz. **104:** 323–328. *f. 1–13.* 8 Ja 1943.

Rick, C. M. The genetic nature of *X*-ray induced changes in pollen. Proc. Nat. Acad. **28:** 518–525. D 1942.

Roberts, L. M. The effects of translocation on growth in *Zea mays*. Genetics **27:** 584–603. N 1942.

Skirm, G. W. Bivalent pairing in an induced tetraploid of *Tradescantia*. Genetics **27:** 635–640. N 1942.

Sparrow, A. H. Non-random uncoiling in heterobrachial chromosomes. Proc. Nat. Acad. **28:** 463–467. N 1942.

Sparrow, A. H., Ruttle, M. L. & Nebel, B. R. Comparative cytology of sterile intra- and fertile intervarietal tetraploids of *Antirrhinum majus* L. Am. Jour. Bot. **29:** 711–715. *f. 1–7.* 13 D 1942.

Stair, E. C. & Showalter, R. K. Tetraploidy in tomatoes induced by the use of colchicine. Proc. Am. Soc. Hort. Sci. **40:** 383–386. *f. 1, 2.* My 1942.

Swanson, C. P. & Nelson, R. Spindle abnormalities in *Mentha*. Bot. Gaz. **104:** 273–280. *f. 1–20.* 8 Ja 1943.

Yarnell, S. H. Leaf segregation in citrus-poncirus hybrids. Proc. Am. Soc. Hort. Sci. **40:** 259–263. My 1942.

MYCOLOGY AND PHYTOPATHOLOGY

Azevedo, N. da S. Herbario micológico do Jardim Botânico. Rodriguesia **6**[15]: 69–81. Je 1942.

Bedford, C. L. A taxonomic study of the genus *Hansenula*. Mycologia **34:** 628–649. 2 D 1942.

Bonar, L. & Cooke, W. B. Some new and interesting fungi from Mount Shasta. Mycologia **34:** 663–668. 2 D 1942.

Braun, A. C. & Laskaris, T. Tumor formation by attenuated crown-gall bacteria in the presence of growth-promoting substances. Proc. Nat. Acad. **28:** 468–477. *f. 1–3.* N 1942.

Brodie, H. J. Protoplasmic continuity in the powdery mildew *Erysiphe graminis* DC. Canad. Jour. Res. C. **20:** 595–601. *pl. 1 + f. 1–7.* D 1942.

Brooks, T. E. Myxomycetes of Kansas—II. Stemonitales. Trans. Kansas Acad. **45:** 59–70. 1942.

Clayton, C. N. The germination of fungous spores in relation to controlled humidity. Phytopathology **32:** 921–943. *f. 1–9.* N 1942.

Couch, J. N. A new fungus on crab eggs. Jour. Elisha Mitchell Soc. **58:** 158–161. *pl. 18, 19.* D 1942.

Cummins, G. B. Descriptions of tropical rusts—V. Bull. Torrey Club **70:** 68–81. *f. 1–11.* 2 Ja 1943.

Cummins, G. B. Revisionary studies in the tropical American rusts of *Panicum*, *Paspalum* and *Setaria*. Mycologia **34:** 669–695. *f. 1–24.* 2 D 1942.

Davidson, R. W. Some additional species of *Ceratostomella* in the United States. Mycologia **34:** 650–662. *f. 1–4.* 2 D 1942.

Demaree, J. R. & Wilcox, M. S. Blueberry cane canker. Phytopathology **32:** 1068–1075. *f. 1–3.* D 1942.

Dickson, J. G. Outline of diseases of cereal and forage crop plants in the northern part of the United States. i–vii, 1–259. lithoprinted. Burgess Pub. Co., Minneapolis. 1940.

Doolittle, S. F. & Beecher, F. S. A strain of tobacco-mosaic virus causing a necrosis and shriveling of tomato foliage. Phytopathology **32:** 986–994. *f. 1–2.* N 1942.

Drechsler, C. Antagonism and parasitism among some oomycetes associated with root rot. Jour. Wash. Acad. **33:** 21–28. *f. 1–3.* 15 Ja 1943.

Drechsler, C. Two zoophagous species of *Acrostalagmus* with multicellular *Desmidiospora*-like chlamydospores. Jour. Wash. Acad. **32:** 343–350. *f. 1–2.* 15 N 1942.

Elmer, O. H. Effect of environment on the prevalence of soil-borne *Rhizoctonia.* Phytopathology **32:** 972–977. N 1942.

Harrison, C. H. Longevity of the spores of some wood-destroying *Hymenomycetes.* Phytopathology **32:** 1096, 1097. D 1942.

Hills, P. L. The mycelium of the Uredinales. Am. Midl. Nat. **28:** 756–760. *f. 1–5.* N 1942 [10 Ja 1943].

Holmes, F. O. Quantitative measurement of a strain of tobacco-etch virus. Phytopathology **32:** 1058–1067. *f. 1–3.* D 1942.

Johnston, C. O. Notes on plant diseases in Kansas in 1941. Trans. Kansas Acad. **45:** 107–110. 1942.

Kendrick, J. B. & Snyder, W. C. *Fusarium* wilt of radish. Phytopathology **32:** 1031–1033. N 1942.

Kendrick, J. B. & Snyder, W. C. *Fusarium* yellows of beans. Phytopathology **32:** 1010–1014. N 1942.

Koepper, J. M. Relative resistance of alfalfa species and varieties to rust caused by *Uromyces striatus.* Phytopathology **32:** 1048–1057. *f. 1–4.* D 1942.

Lorenz, O. A. & Knott, J. E. Studies of gray-wall of tomato. Proc. Am. Soc. Hort. Sci. **40:** 445–454. *f. 1–2.* My 1942.

Lowe, J. L. The Polyporaceae of New York State (except *Poria*). Bull. N. Y. State Coll. Forestry Tech. Publ. 60: 1–128. My 1942.

McColloch, L. P. An apple rot fungus morphologically related to a human pathogen. Phytopathology **32:** 1094, 1095. D 1942.

Martin, G. W. Taxonomic notes on *Myxomycetes.* Mycologia **34:** 696–704. *f. 1–3.* 2 D 1942.

Mead, H. W. Environmental relationships in a seed-borne disease of barley caused by *Helminthosporium sativum* Pammel, King and Bakke. Canad. Jour. Res. C **20:** 525–538. N 1942.

Pady, S. M. Distribution patterns in *Melampsorella* in the National forests and parks in the western states. Mycologia **34:** 606–627. *f. 1–3.* 2 D 1942.

Pryor, D. E. & Whitaker, T. W. The reaction of cantaloupe strains to powdery mildew. Phytopathology **32:** 995–1004. *f. 1.* D 1942.

Riker, A. J. & Baldwin, I. L. Names for the bacterial plant pathogens. Chron. Bot. 7: 250–252. D 1942.

Ruiz, O. M. Contribucion al conocimiento de las Levaduras del aguamiel y del pulque. An. Inst. Biol. Mexico **13:** 1–21. *f. 1–10.* 1942.

Rupert, J. A. & Leach, J. G. Willow blight in West Virginia. Phytopathology **32:** 1095, 1096. D 1942.

Samson, R. W. & Imle, E. P. A ring-spot type of virus disease of tomato. Phytopathology **32:** 1037–1047. *f. 1, 2.* D 1942.

Seavor, F. J. The mycoflora of Bermuda. Science **96:** 462, 463. 20 N 1942.

Shanor, L. & Conover, R. A. A new *Protoachlya.* Am. Midl. Nat. **28:** 746–751. *f. 1–27.* N 1942 [10 Ja 1943].

Smith, C. O. Crown gall on species of Taxaceae, Taxodiaceae, and Pinaceae, as determined by artificial inoculation. Phytopathology **32:** 1005–1009. *f. 1–3.* N 1942.

Stanley, W. M. The preparation and use of tobacco mosaic virus containing radioactive phosphorus. Jour. Gen. Physiol. **25:** 881–890. *pl. 8, 9.* 20 Jl 1942.

Starr, M. P. & Pirone, P. P. *Phytomonas poinsettiae* n. sp., the cause of a bacterial disease of *Poinsettia.* Phytopathology **32:** 1076–1081. D 1942.

Stevenson, F. J. *et al.* Potato-scab gardens in the United States. Phytopathology **32:** 965–971. N 1942.

Tervet, I. W. & Hart, H. Variation in reaction of Anthony oats to stem rust, *Puccinia graminis avenae.* Phytopathology **32:** 1087–1090. *f. 1.* D 1942.

Valleau, W. D. Control of the common mosaic disease of tobacco by breeding. Phytopathology **32:** 1022–1025. N 1942.

Viégas, A. P. Notas sobre *Polyporus sapurema* Möller. Rodriguesia **6**[15]**:** 57–60. *f. 1–24.* 15 Je 1942.

Wehmeyer, L. E. Contributions to a study of the fungous flora of Nova Scotia. VI. Pyrenomycetes. Canad. Jour. Res. C **20:** 572–594. *f. 1–18.* D 1942.

Wernham, C. C. *Epichloe typhina* on imported fescue seed. Phytopathology **32:** 1093. D 1942.

Wolf, F. T. The microbiology of the upper air. Bull. Torrey Club **70:** 1–14. *f. 1–2.* 2 Ja 1943.

Woods, M. W. Respiration and virus diseases. Chron. Bot. **7:** 243, 244. D 1942.

PALEOBOTANY

Andrews, H. N. Contributions to our knowledge of American carboniferous floras: V. *Heterangium.* Ann. Mo. Bot. Gard. **29:** 275–282. *pl. 25 + f. 1, 2.* 18 D 1942.

Andrews, H. N. & Pannell, E. A fossil Araucarian wood from western Wyoming. Ann. Mo. Bot. Gard. **29:** 283–286. *pl. 26.* 18 D 1942.

Hansen, H. P. A pollen study of a montane peat deposit near Mount Adams, Washington. Lloydia **5:** 305–313. D 1942.

Pannell, E. Contributions to our knowledge of American carboniferous floras: IV. A new species of *Lepidodendron.* Ann. Mo. Bot. Gard. **29:** 245–274. *pl. 18–24.* 18 D 1942.

Sears, P. B. Xerothermic theory. Bot. Rev. **8:** 708–736. D 1942.

ECOLOGY AND PLANT GEOGRAPHY

(See also under Plant Physiology: **McIlvanie**)

Boyd, I. L. Evaluation of species of prairie grasses as interplanting ground covers on eroded soils. Trans. Kansas Acad. **45:** 55–58. 1942.

Clements, F. C. Cycles and climaxes. Chron. Bot. **7:** 241–243. D 1942.

Cressler, L. The effect of different intensities and times of grazing and the degree of dusting upon the vegetation of range land in West Central Kansas. Trans. Kansas Acad. **45:** 75–91. *f. 1–17.* 1942.

Griswold, S. B. A study of the woody plants along the streams which cross Ellis County, Kansas. Trans. Kansas Acad. **45:** 98–106. *f. 1–6.* 1942.

Lacey, M. L. The effect of climate and different grazing and dusting intensities upon the yield of the short-grass prairies in western Kansas. Trans. Kansas Acad. **45:** 111–123. *f. 1–9.* 1942.

Laessle, A. M. The plant communities of the Welaka area, with special reference to correlations between soils and vegetational succession. Univ. Fla. Biol. Sci. Ser. **4**[1]**:** 1–143. *pl. 1–11 + f. 1–25.* 1942.

Larson, F. & Whitman, W. A comparison of used and unused grassland mesas in the badlands of South Dakota. Ecology **23**: 438–445. *f. 1–2.* O 1942.

Lindeman, R. L. The trophic-dynamic aspect of ecology. Ecology **23**: 399–418. O 1942.

Lunsford, W. A. The relation of depth of planting to the morphology of the wheat seedling. Trans. Kansas Acad. **45**: 124–128. *f. 1–2.* 1942.

Mueller, I. M. & Weaver, J. E. Relative drought resistance of seedlings of dominant prairie grasses. Ecology **23**: 387–398. *f. 1–5.* O 1942.

Oosting, H. J. & Reed, J. F. The establishment of a white birch community on cutover pulpwood land in northwestern Maine. Bull. Torrey Club **69**: 647–660. 2 D 1942.

Thomson, J. W. Plant succession in abandoned fields in the central Wisconsin sand plain area. Bull. Torrey Club **70**: 34–41. *f. 1–5.* 2 Ja 1943.

Turner, G. T. & Costello, D. F. Ecological aspects of the pricklypear problems in eastern Colorado and Wyoming. Ecology **23**: 419–426. *f. 1–5.* O 1942.

GENERAL BOTANY
(including biography)
(See also under Taxonomy: **Turrell**)

Anderson, E. & Blanchard, F. D. Prehistoric maize from Cañon del Muerto. Am. Jour. Bot. **29**: 832–835. *f. 1–4.* D 1942 [18 Ja 1943].

Asmous, V. C. Karelin (1801–1872) and Kirilov (1821–1842) explorers of Siberia and Middle Asia. Jour. Arnold Arb. **24**: 107–117. Ja 1943.

Brade, A. C. Excursão à Serra do Caparao. Rodriguesia 6[15]: 87–92. *pl. 1–4 + f. 1–22.* 15 Je 1942.

Calvey, M. E. A study of a few of the medicinal plants found in Cattaraugus County, N. Y. Sci. Stud. St. Bonaventure Coll. **11**[1]: 4–11, 28. Je 1943.

Copeland, E. B. Edible ferns. Am. Fern Jour. **32**: 121–126. *1 pl.* 14 Ja 1943.

Dachnowski-Stokes, A. P. The moss peat situation in relation to national emergency needs. Chron. Bot. **7**: 245–247. D 1942.

Fuchs, W. The possibilities of making coal and oil from plant materials of recent origin. Chron. Bot. **7**: 247–249. D 1942.

Grout, A. J. Severin Rapp; as I remember him. Bryologist **45**: 179, 180. D 1942.

MacDaniels, L. H. Notes on the pollination of the Italian prune. Proc. Am. Soc. Hort. Sci. **40**: 84–86. My 1942.

Mains, A. Joseph Charles Arthur (1850–1942). Mycologia **34**: 601–605. *port.* 2 D 1942.

Morton, C. V. & Schultes, R. E. Localidades visitadas y rutas recorridas por E. W. Nelson en el estado de Oaxaca. An. Inst. Biol. Mexico **13**: 47–51. *port.* 1942.

Robbins, W. W. Francis Ramaley (1870–1942). Ecology **23**: 385, 386. *port.* O 1942.

Smith, G. M. *et al.* A textbook of general botany. 4th ed. x, 1–668 p. *f. 1–459.* Macmillan, New York. 1942.

Tschudy, R. H. & Sargent, M. C. Agar-bearing seaweeds at La Jolla, California. Science **97**: 89, 90. 22 Ja 1943.

Waller, A. E. Dr. John Milton Bigelow, 1804–1878, an early Ohio physician-botanist. Ohio Arch. & Hist. Quarterly **51**: 313–331. Ap 1942.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 3, pp. 213–235 MAY, 1943

THE TERTIARY CHARACTER OF THE COVE HARDWOOD FORESTS OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK[1]

STANLEY A. CAIN

It is the purpose of this paper to show by indirect means that large numbers of the genera of the cove hardwood forests are ancient genera whose species have long lived in the southern Appalachian region. In order to develop the probability of this thesis, it is necessary to make certain assumptions. Direct evidence is lacking.

Abundant fossils of angiospermous forms appear in the Cretaceous, and in the later Cretaceous the flora had become pretty thoroughly modernized with respect to families and genera of flowering plants. Throughout the long history of angiospermous evolution, the southeastern highlands of the United States have been continuously available for occupancy by plants. At longer or shorter intervals of time during this period overland highways have been available for plant migration. The modern flora shows relationships with the south—the Caribbean, Mexico, and Central and South America—, with the north, and, by means of northern routes, with western American, eastern Asia, and Europe. Plant genera which undoubtedly originated elsewhere have found their way into the southern states; and from this area migrations have carried some stocks to remote regions. At other times connections have been broken by encroachment of seas upon the land—as by the Mississippi Embayment—or by ice from the north. Continental shelves have been submerged and coastal plains built up.

Unfortunately, however, the fossil record during this time is absent for the southern highlands themselves. It is only by indirection that we can know the nature of the flora of this region. Rather abundant Cretaceous and early and middle Tertiary fossils are available in the southeastern states, but only for lowland floras where land and sea have met and suitable sedimentary basins have been available.

Of the 81 genera that made their appearance in the Eocene Wilcox flora, 60 per cent are tropical in their modern affinities, and probably also in their ancestry, according to Berry (1930). The Oligocene, he said (Berry 1923), was "a time of tropical marine deposits along the southern coast." And although the "Miocene was pre-eminently the period of hardwood forests," the upland flora was undoubtedly scantily represented in the coastal deposits.

[1] Contribution from the Department of Botany, The University of Tennessee, New Series No. 59.

The tables are published with the assistance of the Lucien M. Underwood Memorial Fund.

[The BULLETIN for March (70: 91–212) was issued March 1, 1943]

In the following tables and calculations of percentages only fossil records from the southeastern states have been considered. Had records from western North America, Greenland, Europe, and Asia been employed, many additional genera could be added to those known from the Cretaceous and Tertiary of the southeastern states. It seems reasonable to assume, however, that several genera of more northern areas, characteristic of temperate and cool temperate climates, must have found their way southward in the uplands even while the shores of the Gulf were clothed by species of *Ficus, Cinnamomum, Laurus*, and other genera of warm temperate and subtropical nature. This assumption is warranted by the observation of modern distributions. For example, red spruce that reaches sea level in Maine does not go lower than 4–5,000 feet in the Great Smoky Mountains. At lower latitudes the same species or ecologically equivalent plants must live at higher altitudes in order to find environmental conditions to which they are adapted.

It is assumed, then, that the incomplete record of modern southern Appalachian genera in the Cretaceous and Tertiary deposits of the southeastern states is not necessarily due to their absence from the southeastern states (or from their chance absence from such floras as the Wilcox, or their lack of discovery as fossils), but is due to their remoteness in the southern uplands from suitable sedimentary basins. It seems to be more surprising that as many temperate genera occur as do, rather than that certain ones are absent from the fossil records. What chance, for example, would *Picea rubens* and *Abies Fraseri* of the present boreal forest of the Smokies have to enter a modern sedimentary basin at low elevation?

The use of the latitude-altitude relation is based on the assumption that the species of the past had approximately the same climatic requirements as do species of the same genera today. Generally this assumption is valid although it is well known that tropical genera and families may have occasional truly temperate forms, or the reverse, that temperate genera and families may have some tropical representatives. This assumption is at the heart of the principle of synchronization in the dating of geological floras as discussed by Chaney (1936). For example, when the Eocene redwood forest was in Alaska, a subtropical flora occupied Washington and Oregon. By Miocene time the redwood forest had migrated down the coast to replace the subtropical, but undoubtedly many of the temperate forms of the Miocene redwood forest of the John Day basin came not only down from the north but also down from higher elevations of approximately the same latitude. This ecological interpretation is valid, but the assumption that all deposits with the same flora are synchronous is not valid.

The second major assumption involved in the present thesis is that the ancient nature of certain genera can be deduced from modern areas. It is

not the size of a generic area that is important, but whether the total area is interrupted by major disjunctions wider than the dispersal capacities of the forms concerned. For example, on the American and Eurasian continents the Pleistocene ice sheets produced disjunctions of once transcontinental ranges. Western and eastern American species of several genera are no longer in contact, and many genera once in western as well as eastern North America are no longer represented west of the Great Plains (Fernald 1925). Similarly, many species were forced to withdraw from great portions of their Eurasian ranges with the continental ice advances and, especially in Europe, there was considerable extinction (Lippmaa 1938).

Long before the Pleistocene, however, the break-up of once circumboreal ranges had commenced in certain regions. From the London Clay flora, for example, it is seen that the subtropical elements were withdrawing from western Europe and being replaced by temperate forms; and in the later Tertiary many of the temperate ranges were disrupted. In America the disruption of transcontinental ranges had been going on steadily with the progressive desiccation of the continental interior by the barrier to the moisture-laden winds from the west formed by the Cordilleras.

Whatever the time of the transoceanic connections (whether by land bridges, as was undoubtedly the case in more recent times, or by continental displacement), two points are clear. In the first place, such connections across the north Pacific and the north Atlantic undoubtedly once existed; and second, climatic conditions were more favorable than now, because temperate plants can only migrate through regions of temperate climate. Demonstration of a land bridge does not prove a migratory tract— conditions must be suitable for the plants under consideration.

It is thus reasonable to assume that certain types of modern areas could only have been attained in Cretaceous and early Tertiary times. This applies with conspicuous reasonableness to those genera which today have species only in eastern North America and in eastern Asia; and applies with only slightly less certainty to those genera that have species of circumboreal area. As a matter of fact, in the absence of fossil records, it is only of those genera that are strictly American endemics, and especially when confined to the Atlantic half of the continent, that one cannot certainly say that they are as old as the Tertiary.

The assumption has been made that many temperate genera not known from the early Tertiary deposits of the southeastern states existed in that region at higher elevations than the floras represented by the Wilcox. It is necessary, then, to consider whether such uplands probably existed, for if there is evidence of their presence the assumption that they were covered by a temperate flora has a high degree of probability. It is true that when subtropical and warm temperate floras were in the lowlands of the south-

eastern states warm types also penetrated low-lying areas much farther northward, as at Brandon, Vermont. Synchronous with these invasions was a northward extension of temperate types to relatively high latitudes. At the same time there must have been an upward migration in mountainous regions of all vegetational belts. The problem, then, is whether there were in the southern states any land masses of sufficient elevation to have supported temperate floras during the early Tertiary and permitted an interdigitation of climatically different floras.

This seems to be a difficult question to answer, but some indication of the situation is obtainable from Wright (1932). The oldest erosion surface that is well preserved in this region is the Schooley peneplain. This erosion level stands today at about 3,100 feet at Pisgah and 4,000 feet near Grandfather Mountain, North Carolina. Certain mountain groups, supposedly as monadnocks, rise above the well developed Schooley level in nearby areas. For example, Grandfather Mountain now rises about 2,000 feet above the Schooley level, and Blue Ridge and Great Smoky Mountain peaks rise from 1,000 to more than 3,000 feet above the Schooley level at Pisgah. In addition to this differential in altitude, which may be conservatively placed at 2,000 feet, it is certain that the monadnocks were even higher above sea level. In places the slope of the Schooley peneplain appears to have been as much as 70 feet in a mile. Although its average slope was probably much less, it seems probable that the upper edge of the plain must have stood at somewhat more than 1,000 feet above sea level. There may have been some differential uplift which has made the Blue Ridge and other monadnocks higher now than they were in Schooley time. It does not seem unreasonable, however, to conclude that various monadnocks such as the Cumberland Mountains, the Great Smoky Mountains, and the Blue Ridge must have stood from 1,000 to 3,000, or even 4,000 feet above sea level. Two further questions need to be considered. Are these probable elevations sufficient to have permitted a temperate montane flora when the lowlands were occupied by warm temperate and subtropical floras? Were these elevations in existence during early Tertiary time?

Wright (1932) suggests that the Schooley is possibly Cretaceous. Cole (1941), who has studied the various erosion surfaces and made correlations of them, accepts the conclusion of Stose (1940) that the development of the Schooley surface can probably be assigned to the Jurassic, although the maximum dissection of this surface may not have occurred until mid-Tertiary. It is possible to conclude, then, that the Schooley was undergoing elevation during the Cretaceous and early Tertiary, and that the conclusion with respect to the presence of uplands in the southeastern states is fairly sound.

As to the other question, and judging from the altitudinal relations of

modern vegetational belts, it seems likely that the maximum elevations of 3,000 to 4,000 feet above sea level which the more important monadnocks probably had were sufficient to permit the existence of temperate vegetation in a latitude where subtropical floras occurred at sea level. This, as has already been admitted, does not constitute more than circumstantial evidence for the existence of a typical temperate flora in the uplands at Wilcox latitudes, but in view of the fact that the Wilcox does contain some temperate genera, it seems reasonable that the uplands must have contained many of them.

The method of obtaining the data presented below will be described briefly. A list of the arborescent species of the Great Smoky Mountains National Park was obtained from the Park catalogue (Jennison 1938). All other records of the flora are incomplete, because they represent only those plants encountered on sample plots from the cove hardwood forest complex. The list of trees and tabular data were obtained from plots that averaged about 4,000 sq. m. in area from each of 31 stations in the virgin forest of the Greenbrier region. Data concerning shrubs, woody vines, and herbs were obtained from 19 stations. During the spring-flowering season, 10 stations were studied by a series of 10 quadrats of 1 sq. m. each at each station. During the summer season, 9 stations were studied by a series of 10 quadrats of 6 sq. m. each at each station. Although these data do not include all the species of the cove hardwood forest complex, they do represent its characteristic composition in primeval condition.

Fossil records of the genera of the plants that compose the present forest were obtained from various publications concerning the southeastern states. This area is interpreted as extending from the deposits of the eastern shore of the Mississippi Embayment to Florida and northward to Kentucky, New Jersey, and Maryland. The formations consulted are shown in table 1. Only those records which seem certainly to represent modern genera are included. For example, *Gleditsiophyllum* is not accepted as indicating the presence of *Gleditsia*.[2] The publications used were principally those of Berry and Knowlton, and are cited at the bottom of table 7. In the study of modern generic areas Dalla Torre and Harms (1900–1907) provided the standard source of information. This was supplemented by reference to Bailey (1933), Small (1933), and other more recent sources.

If a genus is listed as being present in Asia and America, and absent from Europe, it frequently is confined to eastern Asia and eastern North America. Some species may occur also in the Himalayas or western North America, or in the south temperate zone. These additional areas do not affect the point made, that the genus has major disjunctions that are substantial

[2] Berry (1930) transferred *Cassia mississippiensis* to *Gleditsia ? mississippiensis* as a tentative disposal of certain Wilcox fossils.

proof of the ancient origin of the generic stock. *Hystrix*, for example, consists of four species in North America, Siberia, and New Zealand. *Vagnera* is in Asia and both western and eastern North America. *Arisaema* is in Asia, Abyssinia, and North America. *Podophyllum* is in America and the Himalayas. *Meibomia* is in America, Asia, and Australia. Sometimes the present disjunctions are partially bridged by fossil records. Section *Saccharina*, of *Acer*, according to Pax (1926), was represented in Europe and Pacific North America during the Tertiary. Today the section (or the genus *Saccharodendron*) consists of *A. saccharum*, *A. floridanum*, *A. nigrum*, and *A. leucoderme* in eastern North America, *A. grandidentata* in the Rocky Mountains, and *A. diabolicum* in Japan. A considerable number of the genera not only had an extensive range in the Cretaceous or early Tertiary, but probably also consisted of many more species than today. Not only are several genera represented today by a small number of closely related species in eastern America and eastern Asia, but these relic genera are frequently quite without close relatives. *Caulophyllum* has one species in each region. This is likewise true of *Tovara*, *Diphylleia*, *Sassafras*, and *Liriodendron*. When certain other genera are listed as being circumboreal, in Europe, Asia, and North America, it does not necessarily mean that the genus lacks tropical or south temperate species. *Carpinus*, for example, is also in the temperate of Mexico. *Wallia* (*Juglans*) is also in the West Indies and the Andes of South America. *Alnus* is also in the Andes; and *Morus* and *Ulmus* extend into tropical mountains. *Aster* is in South Africa, as is *Oxalis*. Many genera are practically all over the world, as well as being circumboreal. Here may be mentioned such genera as *Ranunculus*, *Poa*, *Carex*, *Senecio*, *Alsine* (*Stellaria*), *Galium*, *Allium*, *Cuscuta*, *Geum*, *Peramium* (*Epipactis*), etc.

TABLE 1. *Formations of the southeastern states checked for fossil representatives of the modern genera of the cove hardwood forests of the Great Smoky Mountains National Park. From Knowlton (1919).*

Age	Middle Atlantic	South Atlantic	Gulf
Pleistocene	Talbot Sunderland	Chowan Sunderland	
Pliocene			Citronelle
Miocene	Calvert		
Eocene		Barnwell	Claiborne Wilcox Lagrange Midway
Cretaceous, Upper	Monmouth Matawan Magothy Raritan	Black Creek Middendorf	Ripley Eutaw Tuscaloosa Woodbine
Cretaceous, Lower	Patapsco Arundel Patuxent	Patuxent	Trinity

SOME CHARACTERISTICS OF THE COVE HARDWOOD FORESTS

The author has been studying the composition and structure of the virgin cove hardwood forests for the past several years and considerable unpublished data have accumulated. Quantitative studies have been made at over 50 stations, but the data employed in the present connection represent the summary of only 31 stations from the Greenbrier region. Single plots, averaging about 4,000 sq. m. in area, have been used for the arborescent layer. Occasionally the plots have been as small as 3,000 sq. m., or as large as 5,400 sq. m. The size of the plot at any station has been regulated by several factors: the size and density of the dominant species; the number of species in the community; and the homogeneity of the stand, with respect to frequency of the species and their basal area. It is thought that the data obtained from the various plots are more directly comparable, because of the adjustment of plot size to stand character, than if a constant-size plot had been used. Each plot was approximately of minimal area size.

The various subtypes of the cove hardwoods have been arranged in two alliances, the Aesculion and the Tsugion. The following tabulation shows the subtypes in each alliance:

Cove hardwood forest complex (Greenbrier region, Great Smoky Mountains)
- Aesculion
  - Aesculo-Tilietum (buckeye basswood segregate)
  - Saccharodendro Halesietum (sugar maple-silverbell segregate)
  - Betuletum (yellow birch segregate)
  - Fagetum (beech segregate, mostly a high altitude gap type)
- Tsugion
  - Tsugo-Fagetum (hemlock beech segregate)
  - Tsugo Liriodendretum (hemlock tulip tree segregate)
  - Tsugetum (hemlock segregate)

These forest types can be considered association segregates, in the sense of Braun (1935), or lociations, in the sense of Clements (1936) and Cain (1939). Collectively, the cove hardwood forests represent a southern Appalachian faciation of the maple-beech-hemlock-birch association of the eastern deciduous forest formation. The southern faciation is distinguished from the northern forest by the presence of such trees as *Aesculus octandra*, *Halesia monticola*, and *Magnolia Fraseri*, and the abundance of *Liriodendron tulipifera*. Most of the stations studied by quantitative means were selected because of their representation of the subtypes. A larger total acreage is covered by mixed, mesophytic forests that cannot be easily assigned to a subtype. This is the undifferentiated deciduous forest climax of Braun (1935), and others.

The concept is widely prevalent that the so-called Arctotertiary forest was essentially an undifferentiated mixture of a large number of temperate forest species. With relative homogeneity, it presumably occupied an ex-

tensive circumboreal territory, and, during the Tertiary, with climatic deterioration in many places, specific and generic ranges were contracted and disjoined. This process was brought virtually to a modern condition by the Pleistocene ice sheets. It is certainly true, as shown by fossil records as well as modern areas, that many species and genera once occupied more extensive areas; and many regions once had a richer temperate forest flora. For example, many eastern forest genera were once a part of the western American forests, and are now completely unrepresented there. It does not seem correct, however, to emphasize too strongly the undifferentiated character of the Tertiary forests. Inasmuch as there were oceanic and continental areas, low and high elevations, and strong topographic contrasts during the Tertiary, there must also have been local or microclimates. The Tertiary forest must also have had faciations and lociations, as well as larger associations. It is not intended to deny that the undifferentiated forest probably occupied a larger area during the Tertiary than it does today, but to emphasize that association segregates were undoubtedly a feature of the Arctotertiary forest then, even as now. To reason otherwise would be to assume that many species have changed their ecological tolerances, with the passage of time, always in the direction of narrower amplitude.

In table 2 are presented the statistical data concerning the arborescent layer. Density and coverage data are not shown for the purposes of this paper. By present (columns 1 and 3) is meant that the species was found growing within the number of plots indicated. A species was not considered to be dominant unless it composed about 50 per cent or more of the total basal area of the trees on the plot. Codominants are those species of more than about 15 per cent basal area. In most of the stations there were only about from two to four dominants and codominants making up 80 per cent or more of the stand. Constancy per cent is an indication of the occurrence of the species at the stations on a basis of the minimal area plots. From the table it is seen that 12 species are dominant or codominant at various stations in the cove hardwood forest. The two alliances are not distinguished by the presence or absence, but by relative importance of species. The most frequent dominants of the Aesculion are *Aesculus octandra* dominant at 10 stations, *Tilia neglecta* at 9 stations, and *Saccharodendron barbatum* at 8 stations. The most frequent dominants of the Tsugion are *Tsuga canadensis* at 12 stations and *Liriodendron tulipifera* at 9 stations. Twenty additional species are associates of the dominants, and do not attain sufficient coverage at any station to be classified as even a codominant. *Tsuga canadensis, Betula alleghenionsis, Aesculus octandra, Halesia monticola, Tilia neglecta, Saccharodendron barbatum,* and *Fagus grandifolia* have a constancy of class V, being present in the sample plots of more than 80 per cent of all the stands.

Shrubs and woody vines were sampled in the same plots employed for

TABLE 2. *Trees of the cove hardwood forests of the Great Smoky Mountains found on sample plot studies of the Aesculion and Tsugion.*
All genera were in the Southeastern States in Pre-Pleistocene except those marked by an asterisk:

	Aesculion (18)		Tsugion (13)		Cove Hard-woods
	Stations Present	Stations dominant or co-dominant	Stations Present	Stations dominant or co-dominant	Constancy %
Tsuga canadensis	16	4	13	12	93.5
Betula allegheniensis	16	3	10	0	87.1
Aesculus octandra	16	10	11	0	87.1
Halesia monticola	14	3	13	3	87.1
Tilia neglecta	16	9	10	1	83.9
Saccharodendron barbatum	15	8	10	0	80.6
Fagus grandifolia	14	2	11	4	80.6
Fraxinus americana	10	1	9	0	61.3
Liriodendron tulipifera	5	1	9	9	45.2
Padus virginiana	7	1	2	0	29.0
Castanea dentata	3	1	3	1	19.3
Picea rubens	1	0	1	1	6.4
Magnolia Fraseri	3		12		48.4
Rufacer rubrum	3		10		41.9
Acer pennsylvanicum	6		6		38.7
*Tulipastrum acuminatum	6		4		32.2
Hicoria cordiformis	6		2		25.8
Amelanchier laevis	3		5		25.8
Acer spicatum	6		2		25.8
Ilex opaca	0		6		19.3
Quercus maxima	4		1		16.1
Svida alternifolia	3		2		16.1
Betula lenta	0		5		16.1
Hamamelis virginiana	1		2		9.7
Wallia cinerea	2		0		6.4
Ilex monticola	0		2		6.4
Aralia spinosa	0		2		6.4
Cynoxylon floridum	1		0		3.2
Cladrastis lutea	0		1		3.2
*Oxydendrum arboreum	0		1		3.2
Quercus montana	0		1		3.2
*Robinia pseudoacacia	0		1		3.2
Total number of species sampled	24		30		32
Total number of genera sampled	21		26		28
Total Tertiary genera sampled	19		22		24
Per cent genera sampled that are as old as the Tertiary	90.5		84.6		85.7

the herbaceous layer. Ten stations were studied during the spring flowering season, and nine additional stations were examined during the summer. These stations were taken mostly from the Aesculion. Table 3 shows that

TABLE 3. *Shrubs and woody vines of the Great Smoky Mountains found on sample plot studies of the cove hardwoods.*

Those indicated by an asterisk are not known from the Southeastern States as Pre-Pleistocene fossils, but undoubtedly were there during the Tertiary, as shown by modern areas.

	Vernal aspect (10 stations)		Aestival aspect (9 stations)	
	Constancy %	Frequency %	Constancy %	Frequency %
*Rubus canadensis	50	12	89	18
Euonymus obovatus	40	21	44	23
*Parthenocissus quinquefolia	10	1	55	17
Viburnum lantanoides	10	1	33	9
Aristolochia macrophylla	30	5	11	2
Smilax hispida			33	3
Euonymus americanus	10	6	22	12
Hydrangea arborescens	10	1	22	5
Pyrularia pubera	10	1	11	1
*Sambucus pubens	20	2		
Vitis aestivale			11	1
Rubus nigrobaccus			11	1
Grossularia Cynosbati	10	1		

altogether, nine shrubs and four woody vines were found on the plots. These plants are never of very great importance (with respect to frequency, constancy, coverage, or density) in the cove hardwood forest type complex, except locally.

In studying the herbaceous layer, the Pteridophytes were sampled at the same time as the flowering herbs, but it was useful to separate them in presenting the results. Table 4 gives the data for the Pteridophytes. Only *Dryopteris intermedia, Athyrium thelypteroides*, and *Polystichum acrostichoides* were of sufficient constancy or frequency to be of much significance.

Table 5 lists all the flowering herbs encountered in the quadrat studies. They are grouped according to the constancy class to which they attain in either the vernal or the aestival aspect. For example, *Alsine tennesseensis* (conspicuously the most ubiquitous herbaceous species of the cove hardwood forest complex), *Tiarella cordifolia, Aster acuminatus*, and *Anemone quinquefolia* have a class V constancy in both aspects. *Erythronium americanum, Dentaria diphylla*, and *Viola sororia* reach class V in the spring flora, but not in the summer samples. The remaining species had a class V constancy only in the summer plots: *Urticastrum divaricatum, Viola blanda, Solidago Curtisii, Eupatorium urticaefolium*, and *Nabalus*. Such contrasts as are apparent between the vernal and the aestival samples are not all due to aspect, but are largely attributable to the heterogeneity of the herbaceous layer from station to station. Certain species of the spring flora, however, are usually absent from the summer stage, having completed their life-cycles by the time the full canopy of the forest has developed. In this group can

be mentioned *Erythronium americanum*, *Bicuculla canadensis*, *Bicuculla cucullaria*, *Claytonia virginica*, *Phacelia fimbriata*, and *Panax trifolium*. Species that are inconspicuous or have scarcely started their development in the spring, and which are of importance in the summer flora because of their high coverage, include such plants as *Eupatorium urticaefolium*, *Aster acuminatus*, *Urticastrum divaricatum*, *Solidago Curtisii*, *Monarda didyma*, *Impatiens pallida*, etc.

TABLE 4. *Pteridophytes of the Great Smoky Mountains found on sample plot studies of the cove hardwoods.*

Genera marked by an asterisk are not known from the Southeastern States as Pre-Pleistocene fossils, but from their modern areas they were undoubtedly in the region during the Tertiary:

	Vernal aspect (10 stations)		Aestival aspect (9 stations)	
	Constancy %	Frequency %	Constancy %	Frequency %
Dryopteris intermedia	90	36	89	77
Athyrium thelypteroides	60	20	100	45
*Polystichum acrostichoides	50	10	78	15
*Botrychium virginianum	40	5	44	10
Lycopodium lucidulum	40	9	33	13
Dryopteris noveboracense	10	6	55	32
*Botrychium dissectum	10	1	33	5
*Cystopteris fragilis	20	11	22	4
Athyrium asplenioides			22	5
*Botrychium obliquum	20	2		
Dryopteris hexagonoptera	10	5	11	10
Athyrium pycnocarpon			11	3
Osmunda cinnamomea			11	2
Dryopteris marginalis			11	2
Dryopteris dilatata			11	1

The plants of the preceding tables are the ones that are considered later in the development of the thesis that the cove hardwood forest is an ancient forest of essentially Tertiary character. Bryophytic communities of the soil, tree trunks, etc., are not considered at this time. Any one wishing a more complete picture of the cove hardwood forests will find a discussion of the bryophytic communities by Cain and Sharp (1938).

THE TERTIARY CHARACTER OF THE COVE HARDWOOD FOREST

The method of ascertaining the ancient origin of most of the genera of the cove hardwood forest has already been discussed in the introduction. At this point, however, it is necessary to explain why generic units are used rather than species. In a study of Pleistocene plants of the Wicomico, Chowan, and Pamlico stages from North Carolina, Berry (1925b) found that none was foreign to the region as a whole, although several no longer exist at the localities where the fossils were found. Furthermore, only about

TABLE 5. *Species of the herbaceous stratum of the cove hardwood forest type complex of the Great Smoky Mountains National Park as observed from sample plot studies at 19 stations in the virgin forest.*

The vernal and aestival studies were made at different stations, so the differences are not wholly ones of aspect. Ten 1 sq. m. quadrats were used at each of the vernal stations; 10 6 sq.m. quadrats were used at each of the aestival stations. The species indicated by an asterisk are members of genera for which no evidence of their Tertiary nature is at hand. Nomenclature follows Small (1933).

Species are arranged according to the constancy classes to which they attain	Vernal flora		Aestival flora	
	Constancy %	Frequency %	Constancy %	Frequency %
Class V (81–100%)				
Alsine tennesseensis	100	99	100	100
Arythronium americanum	100	75		
Tiarella cordifolia	100	73	89	81
Aster acuminatus	100	61	100	81
Dentaria diphylla	90	55	33	5
Anemone quinquefolia	90	54	100	38
Viola sororia	90	36	78	53
Urticastrum divaricatum	70	34	100	78
Viola blanda	80	59	100	72
Solidago Curtisii	70	39	100	62
Eupatorium urticaefolium	30	21	89	65
Nabalus sp.	60	16	89	33
Class IV (61–80%)				
Bicuculla canadensis	80	41		
Viola hastata	80	35	11	8
Panax trifolium	80	35		
Mitchella repens	80	24	67	37
Caulophyllum thalictroides	80	16	78	25
Claytonia virginica	70	61		
Trillium erectum var. album	70	27	55	12
Cimicifuga americana	60	49	55	17
Oxalis montana	50	22	67	25
Ranunculus recurvatus	40	26	67	22
*Monarda didyma	30	12	67	12
Polygonatum biflorum	40	4	67	10
Class III (41–60%)				
Impatiens pallida	60	26	55	32
Poa cuspidata	60	21	33	14
Osmorrhiza Claytoni	60	16	55	22
Viola canadensis	50	13	11	4
Viola rostrata	50	12	11	1
Galium triflorum			55	29
Disporum lanuginosum	30	9	55	23
Carex flexuosa			55	13
Carex plantaginea	30	5	55	11
*Rudbeckia laciniata	30	12	44	20
Hepatica acuta	30	6	44	17
Tovara virginiana			44	12
*Hydrophyllum canadense	30	3	44	9
*Medeola virginiana	10	2	44	5
Class II (21–40%)				
*Phlox stolonifera	40	15	33	29
*Validallium tricoccum	40	11	33	10
Veratrum viride	30	18		
Arisaema quinatum	30	14	33	9
Carex austro-caroliniana	30	11	22	3
Podophyllum peltatum	30	10		

TABLE 5. (*Continued*)

Species are arranged according to the constancy classes to which they attain	Vernal flora		Aestival flora	
	Constancy %	Frequency %	Constancy %	Frequency %
Galium circaezans	30	7		
*Xeniatrum umbellulatum	30	3	11	1
Cuscuta sp.			33	4
Arisaema triphyllum	10	1	33	4
Viola rotundifolia	20	8	33	3
*Chrosperma muscaetoxicum			22	13
Sedum ternatum	10	3	22	10
Cryptotaenia canadensis			22	9
*Adicea pumila			22	8
*Syndesmon thalictroides			22	5
Viola eriocarpa			22	4
*Campanulastrum americanum			22	3
Geum canadense			22	2
Peramium ophioides			22	2
Vagnera racemosa	20	3	22	2
CLASS I (1–20%)				
*Phacelia fimbriata	20	14		
Viola pallens	20	9		
Viola cucullata	20	8		
Mitella diphylla	20	6	11	3
Geranium maculatum	20	6	11	2
*Zizia Bebbii	20	4	11	9
Lilium superbum	20	2		
Juncoides bulbosum	20	2		
Carex prasina	20	2	11	3
Trillium grandiflorum	10	10	11	3
Actea alba	10	6		
Ranunculus fasicularis	10	4		
Micranthes micranthidifolia	10	4		
*Cymophyllus Fraseri	10	3	11	3
Juncoides saltuense	10	3		
Galium aparine	10	2		
Diphylleia cymosa	10	2		
Ranunculus abortivus	10	1	11	2
*Collinsonia canadensis	10	1		
Circaea latifolia	10	1		
*Heucnera americana	10	1	11	1
Bicuculla cucullaria	10	1		
Senecio Rugelii	10	1		
Clintonia borealis	10	1		
Glycine Apios			11	8
*Taenidia integerrima			11	5
*Blephilia hirsuta			11	5
Solidago axillaris			11	5
Hystrix Hystrix			11	3
*Houstonia purpurea			11	3
Meibomia nudiflora			11	2
Monotropa uniflora			11	1
Juncus tenuis			11	1
Thalictrum dioicum			11	1
Carex pennsylvanica			11	1
Panicum sp.			11	1
Carex stellata			11	1
Asclepias exaltata			11	1
Lysimachia quadrifolia			11	1

four per cent of the species are now extinct (a *Quercus* and a *Dendrium*). The remainder of the flora seems unchanged and includes such dry habitat plants as *Hicoria glabra*, *Quercus prinus*, *Q. velutina*, *Celtis occidentalis*, and *Vaccinium* (*Batodendron*) *arboreum*. Most of the plants are characteristic of moist to wet habitats and include *Taxodium distichum*, *Hicoria aquatica*, *Quercus palustris*, *Q. Michauxii*, *Planera aquatica*, and *Nyssa biflora*. The general practice of paleobotanists seems to be to consider Pleistocene fossils as conspecific with existing forms unless the weight of evidence is to the contrary. With older fossils, however, the opposite practice is the rule. One method that is very helpful in understanding the characteristics of a fossil flora is to indicate the nearest living relatives of the extinct forms. This can be illustrated by the following Miocene list from Berry (1916b), table 6. As far back as the Eocene, there was considerable resemblance

TABLE 6. *A comparison of species from the middle Miocene Calvert flora of Virginia and their closest living relatives. (From Berry 1916b).*

From the Calvert flora	Closest living relative
Salvinia formosa	Salvinia natans
Pinus sp.	Pinus taeda
Taxodium dubium	Taxodium distichum
Quercus calvertonensis	Quercus alba
Carpinus grandis	Carpinus caroliniana
Ulmus basicordata	Ulmus alata
Platanus aceroides	Platanus occidentalis
Cassia toraformis	Cassia Tora

between fossil species and modern ones. In the Wilcox flora (Berry 1930) *Cercis wilcoxiana* is very close to *C. canadensis*, and *Diospyros wilcoxiana* resembles *D. virginiana*. In the upper Eocene of the Claiborne and Jackson floras there are also examples of striking similarity between fossil and modern species (Berry 1924). Such pairs include *Hicoria jacksoniana* and *H. pecan*, *Castanea claibornensis* and *C. dentata*, and *Tilia jacksoniana* and *T. americana*. It is doubtful whether any species exist now that are very close to the Cretaceous floras. Certainly conspecific identity of types should be accepted only with great hesitancy, although many generic sections were established in the Cretaceous. It is apparent, then, that one could not get very far in proving the Tertiary nature of the modern flora of the Smokies by dealing with species.

On a basis of modern areas it would be possible to indicate that many of the cove hardwood species are of ancient origin. For example, in Europe and in eastern North America respectively there are many pairs of very closely related species such as *Oxalis Acetosella* and *O. montana*, *Polypodium vulgare* and *P. virginianum*, *Hepatica triloba* and *H. americana*, that have diverged only slightly. Between plants of eastern Asia and eastern

America for which geographic disjunction has been of long standing, there are some identities, and a striking series of very closely related pairs of species, such as *Caulophyllum robustum* and *C. thalictroides*, *Liriodendron chinense* (= *L. tulipifera* var. *chinense* Hemsl.) and *L. tulipifera*, etc. In other cases there is not a single pair of species, but a small group of closely related ones: *Pyrularia pubera* is represented by two species in the Himalayas, and *Buckleya distichophylla* (a semi-parasite on *Tsuga*) by three species in China and Japan. On this basis, however, it would not be possible to treat all the species of the cove hardwood forests because such close relatives are frequently absent.

Another difficulty, and a very serious one, with the method of geographic distribution applied to species lies in the necessity of critically examining published accounts and herbarium specimens from a taxonomic point of view. Such a procedure is beyond the scope of this paper. It seems sufficient to treat only of genera.

The study of the cove hardwood forests has been supplemented in one respect. Information has been brought together concerning the total arborescent flora of the Park. The genera native within the Park are listed in table 7, together with their fossil record in the southeastern states. This table also indicates those genera that were probably in the same region during the Tertiary, as shown by their modern areas explained above. Of the 67 genera, 36 are known from Cretaceous deposits of the southeastern states, 23 from the Eocene, 14 from the Miocene, and 10 from the Pliocene. From the whole Tertiary, there are records of 31 of these genera. Genera known from the Cretaceous of the region, but not discovered as yet in the Tertiary, were nevertheless probably still in the region during the Tertiary. These include *Strobus*, *Picea*, *Abies*, *Sabina*, *Populus*, *Liriodendron*, *Malus*, *Amelanchier*, *Crataegus*, *Acer*, *Rufacer*, *Sassafras*, *Benzoin*, *Cynoxylon*, *Kalmia*, and *Viburnum*. Altogether, the fossil records show that 46 genera of the arborescent flora of the Smokies were in the southeastern states in Pre-Pleistocene time.

Table 8 summarizes the data of table 7, and, according to the generic treatment of Small, it is seen that a total of 62 genera (93 per cent) date back to the Tertiary in this region. If the more conservative generic treatment found in Gray's Manual is used, the total of Tertiary genera is 96 per cent. Referring back to table 2, which summarizes the cove hardwood trees, we find that 90.5 per cent of the trees of the Aesculion are Tertiary, and that 84.6 per cent of those of the Tsugion are likewise that old. It is of special interest that all the trees that are dominant or codominant belong to genera that are of Tertiary character.

The summary for the flowering herbs (table 9) is especially interesting. Those species which have the highest constancy (Class V) are entirely of

TABLE 7. *Arborescent genera of the Great Smoky Mountains National Park, and their known occurrence as fossils in the southeastern United States during Cretaceous and Tertiary times.*

Genera	Cretaceous	Tertiary			Pleistocene	Pre-Pleistocene as indicated by modern areas
		Eocene	Miocene	Pliocene		
Pinus	x		x	x	x	x
Strobus (Pinus)	x				x	x (Bailey, 1933)
Picea	x				x	x
Tsuga						x
Abies	x					x
Sabina (Juniperus)	x				x	x (Small, 1933)
Wallia (Juglans)	x	x			x	x (Small, 1933)
Hicoria (Carya)		x		x	x	x (Berry, 1923)
Populus	x				x	x
Salix	x	x	x		x	x
Carpinus			x		x	x
Ostrya					x	x
Betula	x			x	x	x
Alnus					x	x
Fagus	x			x	x	x
Castanea		x		x	x	x
Quercus	x	x	x	x	x	x
Morus					x	x
Ulmus			x		x	x
Celtis	x	x			x	x
Asimina		x			x	
Tulipastrum (Magnolia)						
Magnolia	x	x			x	x
Liriodendron	x				x	x (Small, 1933)
Hamamelis						x
Liquidambar		x			x	x
Platanus	x	x	x		x	x
Sorbus (Pyrus)						x (Small, 1933)
Malus	x					x (Small, 1933)
Amelanchier	x				x	x
Crataegus	x				x	x
Prunus	x	x		x	x	x
Padus (Prunus)						x (Small, 1933)
Cercis		x			x	x
Gleditsia		x			x	x
Cladrastis		x				x
Robinia					x	
Rhus	x		x			x
Ilex	x	x	x	x	x	x
Staphylea						x
Aesculus						x (Pax, 1928)
Acer	x				x	x (Pax, 1926)
Saccharodendron (Acer)					x	(Pax, 1926)
Rufacer (Acer)	x				x	x (Pax, 1926)
Negundo (Acer)	x	x				x (Pax, 1926)
Rhamnus	x	x	x			x
Tilia		x			x	x
Malachodendron (Stuartia)						x
Sassafras	x					x (Small, 1933)
Benzoin	x				x	x
Nyssa	x	x	x	x	x	x
Svida (Cornus)	x	x			x	
Cynoxylon (Cornus)	x					

TABLE 7 (*Continued*).

Genera	Cretaceous	Tertiary			Pleistocene	Pre-Pleistocene as indicated by modern areas
		Eocene	Miocene	Pliocene		
Aralia	x	x				x
Clethra					x	x
Rhododendron						x
Kalmia	x					x
Oxydendrum						
Pieris (Andromeda)	x		x			x (Small, 1933)
Batodendron (Vaccinium)					x	
Cyanococcus (Vaccinium)			x		x	x
Diospyros	x	x	x			x
Halesia						x
Fraxinus	x	x	x	x	x	x
Chionanthus						x
Catalpa						x
Viburnum	x				x	x
Total genera 67	36	23	14	10	41	59

The records incorporated in the above table were obtained from the following publications.
CRETACEOUS: Berry (1914, 1919, 1921, 1923, 1925a, 1930), Knowlton (1919).
EOCENE: Berry (1924, 1930), Knowlton (1919).
MIOCENE: Berry (1923, 1916a, 1916b), Knowlton (1919).
PLIOCENE: Berry (1923), Knowlton (1919).
PLEISTOCENE: Berry (1923, 1925b), Hollick (1906), Knowlton (1919).
MODERN AREAS: From Dalla Torre and Harms (1900-1907) unless otherwise indicated; Bailey (1933), Berry (1923), Pax (1926, 1928), Small (1933).

Tertiary character. In the vernal aspect all the species that are over 40 per cent constant belong to genera that were present in the region during the Tertiary. The most striking feature of the table, however, seems to be the

TABLE 8. *Geological status of the arborescent genera of the Great Smoky Mountain National Park.*

	67 genera, according to Small (1933)		59 genera, according to Gray (1907)	
	No.	%	No.	%
Known from the Cretaceous of the Southeastern States	36	54	32	54
Known from the Tertiary of the Southeastern States	31	46	31	53
Known from Pre-Pleistocene of the Southeastern States	46	69	42	71
Known from the Pleistocene of the Southeastern States	43	64	39	66
Pre-Pleistocene, as indicated by modern generic areas	59	88	55	93
Total undoubtedly in the Southeastern States during Tertiary	62	93	57	96

TABLE 9. *The Tertiary character of the herbaceous stratum of the cove hardwood forest types of the Great Smoky Mountains National Park. Pteridophytes excluded.*

Constancy classes of the species (% of stands)	Vernal aspect (10 stations)		Aestival aspect (9 stations)		Total	
	Genera sampled	Per cent Tertiary	Genera sampled	Per cent Tertiary	Genera sampled	Per cent Tertiary
V (81–100%)	7	100	9	100	11	100
IV (61– 80%)	7	100	6	83	12	92
III (41– 60%)	4	100	10	70	12	75
II (21– 40%)	8	62	15	60	19	63
I (1– 20%)	21	76	20	70	34	76

Total number of genera = 76.
Total number of species = 98.

increase of the Tertiary percentage with an increase of constancy through classes II, III, IV, and V. This may be a coincidence, or it may indicate that the species of the more ancient genera are more thoroughly entrenched in these virgin communities than are the species of American endemic genera.

Finally, table 10 brings together the results for all the groups discussed.

TABLE 10. *Summary: Tertiary genera of the cove hardwood forest types of the Great Smoky Mountains National Park, based on sample plot studies at 31 stations in the virgin forest. Data based on Small's (1933) nomenclature.*

Classification	American endemic genera	Genera known from Pre-Pleistocene in Southeastern United States	Presumptive Tertiary genera from modern areas only	Total genera	Per cent of Tertiary genera
Trees					
All trees of the park	5	59	3	67	93
Cove Hardwood species sampled	3	20	5	28	89
Shrubs					
and woody vines	0	7	3	10	100
Herbs					
Ferns	0	4	3	7	100
Flowers	19	3	54	76	75
Totals					
Cove Hardwoods only	23	33	65	121	81[a]

[a] Using Gray's Manual names, the following higher percentages for Tertiary genera are obtained: All trees, 96; cove hardwood trees, 91; shrubs and woody vines, 100; ferns, 100; flowering herbs, 80; all cove hardwood genera, 86.

Using Small's generic designations, 93 per cent of all the arborescent genera of the Park undoubtedly go back to the Tertiary. For the cove hardwoods alone, we have the following results: 86 per cent of the tree genera, 100 per cent of the shrubs and woody vines, 100 per cent of the ferns, and 75 per cent of the flowering herbs are Tertiary. Of the 121 genera of all life-forms, 81 per cent are Tertiary. If Gray's Manual genera are used instead of

Small's, the Tertiary percentages are consistently higher, as indicated at the bottom of table 10. The percentage of endemism is conspicuously higher in the flowering herbs than in any other life-form.

It is not necessary to conclude that all American endemics not known from Cretaceous or Tertiary fossils are of recent origin. It is simply that there are no good means of ascertaining when these stocks arose.

The following paragraphs present more details concerning the geographic distributions of the genera under discussion. The following genera of trees have modern areas with a major disjunction, being present in eastern North America and Asia, and absent from Europe: *Tsuga, Hicoria, Magnolia, Liriodendron, Hamamelis, Liquidambar, Gleditsia, Cladrastis, Saccharodendron, Sassafras, Benzoin, Nyssa, Aralia, Pieris, Halesia, Chionanthus,* and *Catalpa.* To these 17 genera may be added, without taxonomic damage, *Malachodendron,* a finely drawn generic segregate of *Stuartia* (*Stewartia*) which occurs only in eastern North America and Japan. Also, according to Small, *Kalmia* consists of six North American species, but Dalla Torre and Harms recognize the genus also in western India.

A somewhat longer list of genera is typical of the northern hemisphere, principally in temperate regions, and they occur on the continents of America, Europe, and Asia. These genera belong in the same general group of ancient types as the above, but have not suffered as great a terrestrial disjunction. Included here are *Strobus, Pinus, Picea, Abies, Populus, Salix, Carpinus, Ostrya, Betula, Alnus, Fagus, Castanea, Quercus, Morus, Ulmus, Celtis, Platanus, Sorbus, Malus, Amelanchier, Crataegus, Prunus, Padus, Cercis, Rhus, Ilex, Staphylea, Acer, Rufacer, Negundo, Rhamnus, Tilia, Clethra, Rhododendron, Cyanococcus, Diospyros, Fraxinus, Catalpa,* and *Viburnum.* Again without serious taxonomic damage, to these 39 genera can be added *Sabina,* an American segregate of *Juniperus, Wallia,* an American segregate of *Juglans,* and *Svida* and *Cynoxylon,* American segregates of *Cornus.*

This leaves *Asimina, Tulipastrum, Robinia, Oxydendrum,* and *Batodendron* as American endemics. Of these, *Asimina* is known from the Eocene and Pleistocene of the southeastern United States, *Robinia* from the Miocene elsewhere, and *Batodendron* from the Pleistocene of the southeastern United States.

A survey of the herbaceous flowering-plant genera shows the following to have the typical American-Asian disjunction, being absent from Europe, and frequently from western Asia and western America: *Tiarella, Urticastrum, Bicuculla, Panax, Mitchella, Caulophyllum, Claytonia, Trillium, Osmorrhiza, Disporum, Tovara, Arisaema, Podophyllum, Vagnera, Mitella, Diphylleia, Clintonia, Glycine, Hystrix, Meibomia,* and *Monotropa.*

To these 21 genera can be added 36 more that have a circumboreal distri-

bution which was undoubtedly attained in Pre-Pleistocene time: *Alsine, Erythronium, Aster, Dentaria, Anemone, Viola, Solidago, Eupatorium, Nabalus, Cimicifuga, Oxalis, Ranunculus, Polygonatum, Impatiens, Poa, Galium, Carex, Hepatica, Veratrum, Cuscuta, Sedum, Cryptotaenia, Geum, Peramium, Geranium, Lilium, Juncoides, Actea, Micranthes, Circaea, Senecio, Juncus, Thalictrum, Panicum, Asclepias,* and *Lysimachia.*

According to the information at hand, the following 19 genera are American endemics, not having either the trans-Atlantic or the trans-Pacific disjunction: *Monarda, Rudbeckia, Hydrophyllum, Medeola, Phlox, Validallium, Xeniatrum, Chrosperma, Adicea, Syndesmon, Campanulastrum, Phacelia, Zizia, Cymophyllus, Collinsonia, Heuchera, Taenidia, Blephilia,* and *Houstonia.* This list is somewhat longer, being based on Small (1933) and the recognition of certain segregate genera, than if the genera accepted by Dalla Torre and Harms and Gray are used. For example, *Validallium* is a segregate of *Allium, Adicea* of *Pilea, Syndesmon* of *Anemone, Campanulastrum* of *Campanula,* and *Cymophyllus* of *Carex.* Furthermore, *Phlox* is strictly American except for one species that extends from Alaska into Siberia and may have attained its range relatively recently.

DISCUSSION

The so-called Arctotertiary vegetation is known to have extended from Greenland over northern Europe to the northern Urals. It extended also from the middle zone of Asia to Manchuria, Sachalin and northern Japan. In North America it is known to have occurred from Alaska to the Pacific Northwest, and in the Atlantic Northeast. The vegetation of this wide region consisted of deciduous, summergreen trees (mesophanerophytes) with an admixture of evergreen conifers. It probably required a mean annual temperature of about 10° C. The more important genera of the forest include *Fagus, Castanea, Ulmus, Alnus, Betula, Corylus, Populus, Juglans, Carpinus, Liquidambar, Sequoia,* and *Ginkgo.* Although herbaceous fossils are almost non-existent, except for a few aquatics, there are excellent reasons for believing that the deciduous broad-leaved forests had a well developed herbaceous layer very similar to that of today.

The most illuminating and complete study of this problem is by Lippmaa (1938) on the *Galeobdolon-Asperula-Asarum*-Union of Europe. This herbaceous union is composed of plants of the hemicryptophytic and cryptophytic life-forms and requires relatively strong shade in summer, light in springtime during the flowering period, and a mild humus such as is formed under deciduous forest. Lippmaa concluded that it was no chance that the area of the *Galeobdolon*-Union and its relative societies corresponds so well with the area of the temperate Tertiary forests. The herbaceous vegetation undoubtedly has had the same history as the mesophanerophytes, except that

in Europe the tree vegetation suffered more than the herbs during the glacial period. The area of the *Galeobdolon*-Union and its counterparts must have been as wide in the Tertiary as that of the forest formation with which it is associated.

Lippmaa makes use of detailed analyses of the taxonomic relationships of the character and constant species of the *Galeobdolon*-Union, and of their present distributional patterns. He reached the following conclusions: "All character-species and constant-species of the *Galeobdolon-Asperula-Asarum*-Union are ancient forest plants which are often of an isolated systematic position and whose relatives dwell all over Eastern Asia, North America, the Himalayas, and in part in the Caucasus and southern Europe. Several of the species are relic plants occurring in smaller regions separated from the modern main distribution (*Asperula odorata*, *Actea spicata*, *Sanicula europaea*, *Stellaria holstea*, *Asarum europaeum*, *Bromus Beneckenii*, *Carex digitata*). The species of the union already existed in the Tertiary or they were represented by species which today are very closely related. . . . In Eastern Asia and North America plant unions exist which stand very close to the *Galeobdolon-Asperula-Arisaema*-Union; floristically, however, the species list is wholly different. Only single widely distributed species such as *Aruncus silvester* occur as floristic 'binders.' On the other hand there is undoubtedly a very far-reaching agreement with regard to the elementary life-form which is this union's own. So, for example, in all the named unions, the *Anemone* life-form plays a very important role (*Majanthemum*, *Anemone*, *Paris*, *Dentaria*, *Trientalis*, *Trillium* species)."

It seems reasonable to conclude, from all the evidence that has been presented, even without data concerning species, that the virgin hardwood forests of the Great Smoky Mountains National Park are the finest example of temperate Tertiary forests to be found anywhere in the world, except probably in Eastern Asia. This much is certainly true, a botanist familiar with the modern flora of the cove hardwood forests of the Smokies would find himself "at home" among the temperate forests of the Miocene and later Tertiary, could he be transported back in time. The principal difference would be in the presence in the forest of such temperate trees as *Sequoia* and *Ginkgo*, now very restricted.

SUMMARY

1. An extensive list of species of Angiosperms and Pteridophytes of the virgin cove hardwood forests of the Great Smoky Mountains National Park was obtained from sample plot studies at 31 stations. This was supplemented by a complete list of the trees of the Park.

2. From publications on paleobotany it was found that 27 per cent of

the 121 genera (mostly woody plants) are known as fossils from Cretaceous and Tertiary deposits of the southeastern states.

3. In addition to those genera known to have been in the southeastern states during Pre-Pleistocene time, 54 per cent are probably as ancient as the middle or late Tertiary as shown by their modern areas.

4. A break-down of the totals reveals the following percentages of Tertiary genera:

a. All trees of the Park, 93 per cent of 67 genera;
b. Cove hardwood trees sampled, 86 per cent of 28 genera;
c. Cove hardwood shrubs sampled, 100 per cent of 10 genera;
d. Cove hardwood ferns sampled, 100 per cent of 7 genera;
e. Cove hardwood flowering herbs sampled, 75 per cent of 76 genera;
f. All cove hardwood species sampled, 81 per cent of 121 genera.

5. Species of most importance in the cove hardwood forests are almost exclusively members of genera of ancient origin. The forest dominants are exclusively of ancient origin.

6. Species of American endemic genera are seldom of high constancy, frequency, or coverage in the cove hardwood forests.

7. It is not known whether the Great Smoky Mountains flora is richer in ancient plant species than other North Temperate regions, because comparable data are not available, but all evidence indicates that the cove hardwood forests of the Southern Appalachians, which have their maximum development in the Smokies, are very similar to the rich, mesophytic, and once circumboreal Arctotertiary forests.

THE UNIVERSITY OF TENNESSEE
KNOXVILLE, TENNESSEE

Literature Cited

Bailey, L. H. 1933. The standard cyclopedia of horticulture. New York.

Berry, E. W. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. U. S. Geol. Surv. Prof. Paper 84: 1–200.

————. 1916. The Lower Eocene floras of Southeastern United States. U. S. Geol. Surv. Prof. Paper 91: 1-481.

————. 1916a. The physical conditions indicated by the flora of the Alum Bluff formation. U. S. Geol. Surv. Prof. Paper 98: 41–60.

————. 1916b. The physical conditions indicated by the flora of the Calvert formation. U. S. Geol. Surv. Prof. Paper 98: 61–74.

————. 1919. Upper Cretaceous floras of the western Gulf region in Tennessee, Mississippi, Alabama, and Georgia. U. S. Geol. Surv. Prof. Paper 112: 1–177.

————. 1921. The flora of the Woodbine sand at Arthurs Bluff, Texas. U. S. Geol. Surv. Prof. Paper 129: 153–182.

————. 1923. Tree ancestors. Baltimore.

————. 1924. The Middle and Upper Eocene floras of Southeastern North America. U. S. Geol. Surv. Prof. Paper 92: 1–206.

————. 1925a. The flora of the Ripley formation. U. S. Geol. Surv. Prof. Paper 136: 1–94.

————. 1925b. Pleistocene plants from North Carolina. U. S. Geol. Surv. Prof. Paper 140: 97–120.

————. 1930. Revision of the Lower Eocene Wilcox Flora of the Southeastern United States. U. S. Geol. Surv. Prof. Paper 156: 1–144.

Braun, E. L. 1935. The undifferentiated deciduous forest climax and the association-segregate. Ecology **16:** 514–519.

Britton, N. L. & Brown, A. 1913. An illustrated flora of the northern United States, Canada and the British Possessions. New York Botanical Garden.

Cain, S. A. 1939. The climax and its complexities. Am. Midl. Nat. **21:** 146–181.

Cain, S. A. & Sharp, A. J. 1938. Bryophytic unions of certain forest types of the Great Smoky Mountains. Am. Midl. Nat. **20:** 249–301.

Chaney, R. W. 1936. Plant distribution as a guide to age determination. Jour. Wash. Acad. **26:** 313–324.

Clements, F. E. 1936. Nature and structure of the climax. Jour. Ecol. **24:** 252–284.

Cole, W. S. 1941. Nomenclature and correlation of Appalachian erosion surfaces. Jour. Geol. **49:** 129–148.

de Dalla Torre, C. G. & Harms, H. 1900–1907. Genera siphonogamarum ad systema Englerianum conscripta. Leipsig.

Fernald, M. L. 1925. Persistence of plants in unglaciated areas of Boreal America. Mem. Am. Acad. **15:** 239–342.

Hollick, A. 1906. Pliocene and Pleistocene. Maryland Geol. Surv. pp. 217–237.

Jennison, H. M. 1938. A classified list of the trees of the Great Smoky Mountains National Park. Manuscript on File: National Park Office; Univ. Tenn., Library, and Department of Botany.

Knowlton, F. H. 1919. A catalogue of the Mesozoic and Cenozoic plants of North America. U. S. Geol. Surv. Bull. 696: 1–815.

Lippmaa, T. 1938. Areal und Altersbestimmung einer Union sowie das Problem der Charakterarten und der Konstanten. Acta Inst. Horti Bot. Univ. Tart. **6**(2): 1–152.

Pax, F. 1926. Gesamtareal der Gattung *Acer* und einiger Sektionen.-Verbreitung einiger Sektionen der Gattung *Acer* zur Tertiärzeit. Die Pflanzenareale. 1 Reihe, Karte 4, Heft 4.

————. 1928. Hippocastanaceae DC. Die Pflanzenareale. 2 Reihe, Heft 1, Karte 8.

Robinson, B. L. & M. L. Fernald. 1908. Gray's New Manual of Botany. New York.

Small, J. K. 1933. Manual of the southeastern flora. New York.

Stose, G. W. 1940. Age of the Schooley Peneplain. Am. Jour. Sci. **238:** 461–476.

Wright, F. J. 1932. The older Appalachians of the South. Denison Univ. Bull., Jour. Sci. Lab. **26:** 143–250.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 236–243 MAY, 1943

A POLLEN STUDY OF TWO BOGS ON ORCAS ISLAND, OF THE SAN JUAN ISLANDS, WASHINGTON[1]

HENRY P. HANSEN

INTRODUCTION

The San Juan Islands lie between the mainland of the state of Washington and the southern end of Vancouver Island, about 75 miles from the Pacific Ocean through the Strait of Juan de Fuca. Orcas Island is one of the largest and most northern of the group. It is about 11 miles in extent from east to west, and about 9 miles from north to south. The highest point is Mt. Constitution with an elevation of about 2400 feet. The San Juan Islands were glaciated during the Pleistocene (Bretz 1913), and the higher areas are rocky with little soil. Lower areas near sea level are covered with glacial drift and glacio-lacustrine and glacio-fluviatile deposits. The climate of the San Juan Islands is mild and somewhat drier than that of the Puget Lowland to the east and south. The mean annual precipitation at Olga, at the southern tip of Orcas Island, is about 29.5 inches, and at the north end of East Sound it is slightly over 30 inches. (Climatic Summary, U. S. D. A., 1936.) At San Juan, on San Juan Island, a few miles to the west and south, the mean annual precipitation is about 22.5 inches, while at Anacortes on the mainland to the southeast it is about 27 inches. About 15 per cent of the precipitation occurs during the growing season. In some areas the porosity of the soil permits rapid drainage, whereas in others the absence of much soil results in rapid run-off. The prevailing winds are from the west.

LOCATION AND CHARACTERISTICS OF THE BOGS

One of the bogs is located near the summit of Mt. Constitution on the northeastern part of the island, while the other is situated near sea level at the southern end of the island. There are several bogs on Mt. Constitution, one of which has been described by Rigg and Richardson (1934). The one of this study is several acres in extent and is covered largely with sedge (*Carex* spp. and *Cyperus* sp.) and Labrador tea (*Ledum groenlandicum*). Other of the more common plants are hardhack (*Spiraea douglasii*), salal (*Gaultheria shallon*), cottongrass (*Eriophorum chamissonis*), sundew (*Drosera rotundifolia*), and twinflower (*Linnaea borealis americana*). Trees on the bog in their apparent order of invasion are lodgepole pine (*Pinus contorta*), western hemlock (*Tsuga heterophylla*), and Sitka spruce (*Picea sitchensis*), the first being the most abundant.

[1] Published with the approval of the Monographs Publication Committee, Oregon State College, as Research Paper No. 72, School of Science, Department of Botany.

The lowland bog is situated at the west end of Killebrew Lake, about three-quarters mile north of Grindstone Bay, and about 10 miles southwest of Mt. Constitution. The lake supports various stages of hydrarch plant succession, including submerged, floating, and cattail-bulrush associes. On the bog grow purple marshlocks (*Potentilla palustris*), buckbean (*Menyanthes trifoliata*), spike-rush (*Eleocharis acicularis*), and *Dulichium arundinaceum*. Many other species of bog and marsh plants are present, but those mentioned seem to be characteristic of the associes.

Peat samples were obtained at quarter-meter intervals with a Hiller peat borer. The depth of the Mt. Constitution bog is 9 meters in the area of sampling, and the Killebrew Lake bog is 9.5 meters deep. A stratum of volcanic ash occurs between 7 and 7.5 meters in the montane bog, and at 7 meters in the lowland bog. Ash fragments are scattered throughout a half-meter thickness of peat, but are most abundant at these levels. The relative stratigraphic position of the ash layers is similar to that of most peat profiles in northern Washington, suggesting that the source of the ash was the same volcanic action. According to geologists, the most probable source is Glacier Peak in the Cascades of northern Washington.

In the Mt. Constitution bog, fibrous peat occurs close to the bottom underlain by only a thin stratum of sand and silt resting directly on bedrock. This denotes that the proximity of the original pond to the summit of the mountain prevented the erosion of considerable sand and silt into it, which is often the case in Pacific Northwest bogs. The presence of pollen in these lowest levels, however, indicates that forest invasion of adjacent areas began soon after glacial retreat. The Killebrew Lake bog has a much greater thickness of silt and clay underlying the organic peat. In preparation of the peat for microscopic analysis, the potassium hydrate method was employed. From 100 to 200 pollen grains were identified from each horizon. In identification of the winged conifer pollen, the size range method was used (Hansen 1941a, 1941b, 1941c). The tables showing the percentages of conifer pollen and the number of non-significant pollen grains of herbs, grasses, and deciduous trees are omitted because of the unusual scarcity of the latter. Those species recorded as 1.5 per cent or less are shown on the diagram as 1 per cent.

FORESTS OF THE SAN JUAN ISLANDS

The San Juan Islands lie within the hemlock–cedar climax formation of the Coast Forest (Weaver & Clements 1938). Certain factors of the environment, however, are apparently unfavorable for western hemlock and western red cedar (*Thuja plicata*) to thrive as the principal dominants. These islands are also within the Humid Transition life area (Piper 1906). Forest type maps (1936) show that the San Juan Islands are forested largely with second-growth Douglas fir and subalpine and noncommercial types. Mt. Con-

stitution is forested chiefly with lodgepole pine (*Pinus contorta*), with some Douglas fir (*Pseudotsuga taxifolia*) and western hemlock, and scattered specimens of western white pine (*Pinus monticola*) and lowland white fir (*Abies grandis*). The hills adjacent to the Killebrew Lake bog are forested with second-growth Douglas fir, and some hemlock, lowland white fir, western red cedar, Sitka spruce, and western white pine. The most common broadleaf species are largeleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), and cottonwood (*Populus trichocarpa*). In dry exposed areas on the south slopes, Oregon white oak (*Quercus garryana*) occurs, while the presence of prickly pear (*Opuntia fragilis*) reflects the dryness of the summers.

In the hemlock–cedar formation of the Puget Lowland of western Washington, Douglas fir persists as subclimax and the chief dominant because of recurring fire during the past (Munger 1940). Over much of the area designated as being forested with this association, however, the environment is unfavorable for hemlock and cedar. In some of these areas Douglas fir thrives as the chief dominant even though fire does not occur. It is suggested that the climate is too dry for hemlock to supplant Douglas fir in the course of normal, uninterrupted forest succession (Munger 1940). The east slope of the Coast Range and the Willamette Valley of western Oregon are examples of such regions. Not only is hemlock practically absent at the present time, but pollen profiles from these areas reveal that hemlock has played only a minor role during all or most of the post-Pleistocene (Hansen 1941a, 1942a). Insufficient rainfall is perhaps the main factor inhibiting hemlock from superseding Douglas fir, even in the absence of fire, but the edaphic and topographic conditions may also exercise some control. The annual precipitation in the Willamette Valley is greater than in parts of the Puget Sound region, where hemlock does replace Douglas fir in normal forest succession. The summer precipitation, however, is slightly less and may be the limiting factor in preventing hemlock from invading and assuming predominance. A lower humidity and greater amount of evaporation during the growing season may also be contributing factors. On Orcas Island, then, it seems probable that the annual rainfall, which is slightly less than in the Puget Sound region, and the dry summers are responsible for the comparative absence of hemlock from the forest complex. On the higher parts of the island, the rocky terrain is undoubtedly an additional factor instrumental in its scarcity.

POSTGLACIAL FOREST SUCCESSION

In both areas lodgepole pine was the predominant species when the lowest pollen-bearing sediments were deposited. In the montane bog it is recorded as 71 per cent (fig. 1), and in the Killebrew Lake bog as 69 per cent (fig. 2). The initial postglacial invasion of lodgepole pine in these areas is

consistent with that of many other regions of the Pacific Northwest (Hansen 1938, 1939a, 1939b, 1940a, 1940b, 1941a, 1942a). The trend of lodgepole pine is very different in the two profiles. In the Mt. Constitution bog, lodgepole pine increases from the bottom to 90 per cent at 8 meters, the highest proportion to which it is recorded in any bog thus far studied. It shows a general decrease from this maximum to the surface, fluctuating between 85 per cent at 7.25 meters and 44 per cent at 1 meter, its lowest proportion of the profile. It then increases to 60 per cent at the top. In the Killebrew Lake profile, lodgepole pine diminishes sharply from the bottom to only 7 per cent at 6.5 meters, and from this horizon upward, it fluctuates between 12 and 4 per cent. It is recorded as 6 per cent at the surface. Western white pine is next most abundantly represented, at the bottom and is recorded as 20 and 15 per cent in the montane and lowland bogs respectively (figs. 1, 2). In the Puget Lowland of western Washington, white pine was also one of the predominant pioneer invaders. It diminishes slightly upward from the bottom, but it remains generally constant throughout both profiles, fluctuating between 12 and 1 per cent in the montane bog, and 14 and 1 per cent in the other.

Douglas fir also differs in its successional trends as recorded in the two profiles. In the Mt. Constitution bog, it is recorded as 3 per cent at the bottom, and fluctuates between this and nothing to 6.5 meters (fig. 1). It is then recorded as slowly increasing upward in the profile, reaching its maximum proportion of 30 per cent at 1 meter, and then declining to 15 per cent at the top. In the Killebrew bog, Douglas fir is recorded as 7 per cent at the lowest level, and then increases sharply to its maximum of 67 per cent at 5 meters (fig. 2). It shows a slight decline from this horizon to the surface, where it is represented by 52 per cent of the conifer pollen present.

In the montane bog, western hemlock exhibits somewhat the same general trend as Douglas fir, but it does not reach such high proportions as low in the profile (fig. 1). Its maximum is 30 per cent at 2 meters, and it then diminishes to 17 per cent at the uppermost level. In the lowland bog, hemlock is recorded more abundantly, as is Douglas fir (fig. 2). It increases lower in the profile and attains proportions of 20 per cent at 7.5, 6.5, 4.75, and 3.75 meters, and then declines and remains constant to the top where it is represented by 14 per cent. This species does not reach higher proportions in the Killebrew bog, but it is more consistently represented by greater proportions throughout the profile than in the montane bog.

Other forest trees recorded in appreciable proportions are Sitka spruce and fir. Spruce is represented more abundantly and consistently in the lowland bog (figs. 1, 2). Here its greatest proportion is 9 per cent at the bottom; in the montane bog it attains 7 per cent at 7 meters. This is consistent, because spruce thrives better near the ocean than at higher elevations farther

inland. Fir pollen is listed under the genus only, since the pollen of all species except lowland white fir is only sporadically present. The other species whose pollen was noted are noble fir (*Abies nobilis*), silver fir (*A. amabilis*), and alpine fir (*A. lasiocarpa*). None of these species was noted on Orcas Island, although they may have existed there in the past. Possible sources of their pollen are the other San Juan Islands, Vancouver Island, or the Olympic Peninsula, because of the prevailing westerly winds. Silver and alpine fir are common in the Olympic Mountains, but the occurrence of noble

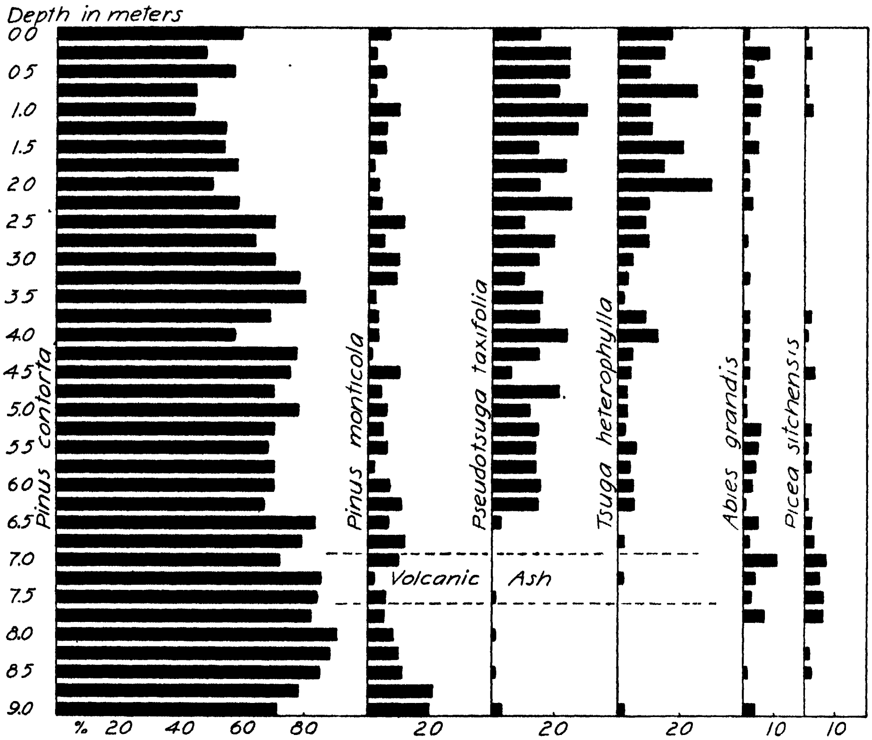


FIG. 1. Pollen profiles. Mt. Constitution bog.

fir is not certain. Noble fir was reported by Sudworth (1908), but Jones (1936) in an extensive study of the flora of the Olympic Peninsula, was unable to find it. This does not exclude the possibility of its existence in the past, and pollen of this species was present in the upper levels of the profiles. A pollen study of a bog on the west side of the Olympic Peninsula also reveals the presence of noble fir pollen, but not in the uppermost level (Hansen 1941d). Fir pollen is more consistently abundant in the Killebrew Lake bog, which is logical because lowland white fir thrives best in low, damp areas. The greatest proportion attained by fir pollen is 16 per cent at 7.25 meters

and at the surface in the lowland bog (fig. 2), whereas in the montane peat deposit it reaches a maximum of 11 per cent at 7 meters and is not present at all horizons (fig. 1). Mountain hemlock (*Tsuga mertensiana*) is sporadically represented in both profiles. Pollen of this species may have come from Vancouver Island or the Olympic Mountains, although it also may have

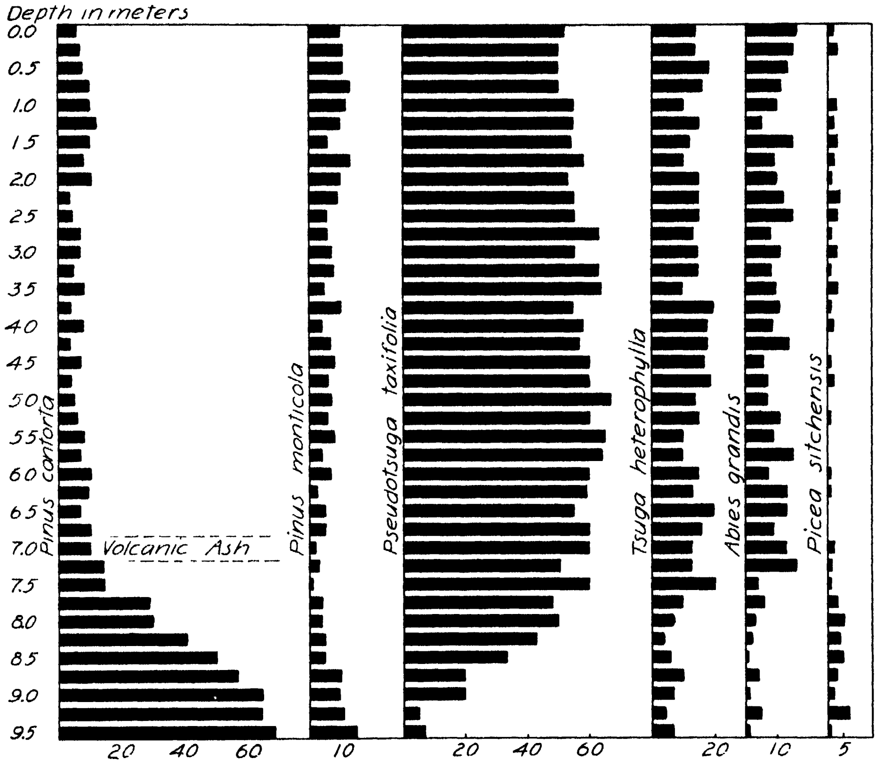


FIG. 2. Pollen profiles. Lake Killebrew bog.

existed in the San Juan Islands earlier in post-Pleistocene time. Broadleaf trees represented by their pollen are red alder and largeleaf maple, both of which are more abundantly recorded in the Killebrew Lake bog. Sedge pollen increases and yellow pondlily pollen diminishes in abundance upward in both profiles, marking the progress of hydrarch plant succession in the bog.

INTERPRETATION OF THE POLLEN PROFILES

The trend of postglacial forest succession in the lowland area of Orcas Island, as portrayed by the pollen profiles of the Killebrew Lake bog, is somewhat similar to that of the Puget Sound region (Hansen 1938, 1940a, 1941a). Pollen analyses of peat deposits there reveal that lodgepole pine was the pioneer postglacial invader and was rapidly supplanted by Douglas fir.

Western hemlock increased more gradually than Douglas fir, but eventually superseded the latter and remained slightly predominant until the advent of white man. In areas adjacent to Killebrew Lake, however, hemlock was never so abundant as in the Puget Sound region, and Douglas fir has maintained a wide degree of predominance since it superseded lodgepole pine. This substantiates the theory that the lack of moisture, particularly in dry summers, on Orcas Island, has prevented hemlock from reaching proportions similar to those in the Puget Sound region. The importance of abundant moisture for the development of hemlock is further corroborated by its predominance in post-Pleistocene forest succession along the Oregon Coast, where the annual precipitation varies from 70 to over 100 inches (Hansen 1941c).

On the summit of Mt. Constitution the thin soil mantle has probably been as important as moisture in controlling forest succession. In fact the rocky terrain, causing rapid run-off, tends to accentuate the dearth of available water for tree growth. Glacial scour left little soil and only a thin layer of residual soil has developed since deglaciation. The much greater intolerance of lodgepole pine for shade than Douglas fir and hemlock, has been compensated for by the edaphic conditions unfavorable for the latter two species. Lodgepole pine has consequently been able to successfully compete with these species. That lodgepole pine is able to thrive under edaphic conditions adverse for other species is shown by its pioneer invasion of areas formerly covered by Pleistocene glaciers in Washington, young sand dunes on the Oregon Coast, climax bogs, pumice mantles in central Oregon, burns, and other edaphically disturbed regions (Hansen 1941c, 1942b, 1942c).

There is little or no evidence for post-Pleistocene climatic trends in the forest succession as portrayed by the pollen profiles. The low proportion of hemlock pollen throughout both profiles in itself, however, denote that it has been too dry for its development to predominance, such as occurred in the Puget Sound region. The rather local representation of the surrounding forests in each respective bog, raises the question as to the size of an area that is represented by its tree pollen in a bog. The small size of the island, restricting the source of the pollen, may tend to accentuate this degree of localization.

SUMMARY

Pollen analyses of two peat deposits on Orcas Island, Washington, reveal different trends of post-Pleistocene forest succession in their respective adjacent areas. In both bogs, lodgepole pine is recorded as having been the predominant, pioneer, postglacial invader. In areas surrounding the montane bog, lodgepole pine maintained predominance throughout the postglacial period to the present. The existing forests are composed chiefly of lodgepole pine. In areas adjacent to the other bog, near sea level, lodgepole

pine was early replaced by Douglas fir which remained predominant during the rest of the post-Pleistocene. The San Juan Islands are located within the hemlock–cedar climax, but hemlock neither superseded nor became nearly so abundant as Douglas fir during the postglacial. This was probably due to the low summer precipitation and the unfavorable edaphic conditions for hemlock. There is little evidence for climatic trends, and it is probable that the ocean has served to maintain an equable climate during postglacial time.

OREGON STATE COLLEGE
CORVALLIS, OREGON

Literature Cited

Bretz, J. H. 1913. Glaciation of the Puget Sound region. Wash. Geol. Surv. Bull. 8: 1–244.

Climatic Summary of the United States. 1936. Western Washington. U. S. Dept. Agric. Washington, D. C.

Forest Type Map. 1936. State of Washington. N. W. Quarter. Pacific N. W. Forest & Range Exp. Sta. U. S. Dept. Agr. Portland, Oregon.

Hansen, H. P. 1938. Postglacial forest succession and climate in the Puget Sound region. Ecology **19**: 528–542.

———. 1939a. Pollen analysis of a bog in northern Idaho. Am. Jour. Bot. **26**: 225–228.

———. 1939b. Pollen analysis of a bog near Spokane, Washington. Bull. Torrey Club **66**: 215–220.

———. 1940a. Paleoecology of two peat bogs in southwestern British Columbia. Am. Jour. Bot. **27**: 144–149.

———. 1940b. Paleoecology of a montane peat deposit at Bonaparte Lake, Washington. Northw. Sci. **14**: 60–69.

———. 1941a. Further pollen studies of post-Pleistocene bogs in the Puget Lowland of western Washington. Bull Torrey Club **68**: 133–148.

———. 1941b. Paleoecology of a peat deposit in west central Oregon. Am. Jour. Bot. **28**: 206–212.

———. 1941c. Paleoecology of two peat deposits on the Oregon Coast. Oregon State Monographs, Stud. Bot. **3**: 1–31.

———. 1941d. Paleoecology of a bog in the spruce-hemlock climax of the Olympic Peninsula. Am. Midl. Nat. **25**: 290–297.

———. 1942a. A pollen study of lake sediments in the lower Willamette Valley of western Oregon. Bull. Torrey Club **69**: 262–280.

———. 1942b. The influence of volcanic eruption upon post-Pleistocene forest succession in central Oregon. Am. Jour. Bot. **29**: 214–219.

———. 1942c. Post-Mount Mazama forest succession on the east slope of the central Cascades of Oregon. Am. Midl. Nat. **27**: 523–534.

Jones, G. N. 1936. A botanical survey of the Olympic Peninsula. Univ. Wash. Publ. **6**: 1–286.

Munger, T. T. 1940. The cycle from Douglas fir to hemlock. Ecology **21**: 451–468.

Piper, C. V. 1906. Flora of the State of Washington. Contr. U. S. Nat. Herb. **11**: 1–637.

Rigg, G. B. & Richardson, C. T. 1934. The development of Sphagnum bogs in the San Juan Islands. Am. Jour. Bot. **21**: 610–622.

Sudworth, G. B. 1908. Forest trees of the Pacific Slope. U. S. Dept. Agr. Washington, D. C.

Weaver, J. E. & Clements, F. E. 1938. Plant Ecology. New York.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 244–251 MAY, 1943

PHYTOPHTHORA ROT OF BELLADONNA[1]

JOHN T. MIDDLETON

INTRODUCTION

With the increasing trend toward the cultivation of pharmaceutical crops, a number of interesting plants and their diseases are encountered. One of the crops recently brought into cultivation again in southern California is belladonna, *Atropa belladonna* L. Of the diseases observed on this host, rot, principally of the root and stem, caused by *Phytophthora parasitica* Dastur, is the most important.

Plantings of belladonna in southern California are confined to small plots, usually from 1 to 10 acres; they are generally coastal and are to be found growing on a number of different soil types. On the heavy, poorly drained soils, root-rot is an important and often limiting factor in growth; on the lighter, adequately drained soils, it is rarely observed and is of little concern.

REVIEW OF LITERATURE

The first record of a root-rot of *Atropa belladonna* is apparently from England, where Barker (1917–1918) reports a *Phytophthora* sp. to be responsible. Westerdijk and van Luijk (1920) later describe a root-rot of belladonna in the Netherlands and state that *P. erythroseptica* Pethyb. is the causal agent. Alcock (1926) records the occurrence of a stem-rot and wilt of belladonna in Scotland and attributes the trouble to *P. erythroseptica* var. *atropae* Alcock. Tucker (1931) does not consider this varietal segregation valid, however, and states that "the reasons for separating the Atropa strain are not very convincing, and, pending further evidence, the writer prefers to include it in *P. erythroseptica*."

Other organisms attack belladonna and cause effects which may be mistaken for those of *Phytophthora* spp. Parisi (1921) reports that *Thielavia basicola* Zopf[2] attacks belladonna in Italy, but adds that infected seedlings recover when planted in the open field in well-aerated soil. MacMillan (1941) reports damping-off of this host, due to *Rhizoctonia* sp. and to *T. basicola*, in California, and describes a root-rot attributed to *Fusarium* sp.; he states that the "mycelium of *Fusarium* is usually found. . . ." No inoculations are recorded.

A preliminary description of the root-rot caused by *Phytophthora* is

[1] Paper No. 478, University of California Citrus Experiment Station, Riverside, California.

[2] Probably *Thielaviopsis basicola* (Berk.) Ferraris, according to McCormick (1925, p. 551).

given by the author (1941) in a short article dealing with several diseases of belladonna in California.

SYMPTOMS OF THE DISEASE

The disease affects fibrous and fleshy roots, crowns, stems, and, to a lesser extent, leaves of the plant. The fungus attacks both fine and larger fibrous roots and causes brown, discolored areas which are at first firm but later become watersoaked and flaccid and subsequently die (fig. 1). The fleshy portion of the root is frequently parasitized; it subsequently turns dark brown to black in color and becomes watersoaked and flaccid. Sunken, necrotic, longitudinally oriented areas, which progress upward into the stem, are often discernible on the outside of the exposed fleshy part of the root (fig. 2).

As root infection progresses upward, other roots and often the crowns of the plants are attacked; incipient shoots that are affected turn dark and die. Frequently the roots of a plant may be badly damaged while the crown remains fairly intact and sends out new shoots; such plants may recover but are of little commercial value. Plants with naturally infected crowns invariably die, being unable to produce new roots; the shoots, becoming infected, turn brown and rot. Sometimes crowns become infected first, and the infection progresses downward to the root and upward into the stem.

Conspicuous, dark, slightly sunken necrotic areas are produced on infected stems. Stems so infected frequently show signs of wilting, the leaves turn yellow, and the plant eventually dies.

Often plants which lack vigor, characterized by yellowed leaves and by some signs of wilting, will show no signs of stem infection. But when such plants are dug and the soil is carefully washed away from the roots, only a few badly infected and discolored roots are found. Sometimes plants are observed to have an abnormally large number of sparsely foliated, slender shoots; the roots and crowns of such plants have also been found to be badly diseased.

Along the coast, under conditions of high relative humidity and warm air temperatures prevalent during the summer months and usually following a foggy period, young shoots and leaves of the plants are attacked, the affected parts collapsing on becoming watersoaked. Through leaf and stem infections the disease may spread throughout the planting.

THE CAUSAL ORGANISM

Phytophthora parasitica was readily obtained in pure culture when tissue plantings of bits of diseased material from the margin of necrotic areas, or from fairly recently infected roots of belladonna plants, were made on cornmeal agar and on plain water agar. The fungus was identified by Dr.

Fig. 1. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced on fibrous roots by *Phytophthora parasitica* 16 days after inoculation in the greenhouse. In addition to the discolored areas on the roots, note the smaller number of roots on the infected plant. Fig. 2. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced on roots and stem by *Phytophthora parasitica* 27 days after inoculation in the greenhouse. The lesion is dark, slightly sunken, and vertically disposed. Note the paucity of roots and the relative size of the shoots in B, as compared with A.

C. M. Tucker. Isolations were typical of the species. *Fusarium* spp. were sometimes obtained in conjunction with *P. parasitica* when infected tissue was taken from badly diseased portions of the plant and plated on these media.

Sporangia of the fungus are typically acrogenous, are infrequently intercalary or borne laterally, and are ovate with a prominent apical papilla; they measure 23.6–49.8 μ by 21.1–36.5 μ, the mean 37.6 μ by 31.0 μ. Oögonia are acrogenous, intercalary or borne terminally on short lateral branches, and from spherical to slightly obovoid, with a smooth wall; in diameter, they measure 19.2–24.9 μ, the mean 22.6 μ. Antheridia are amphigynous. Oöspores are thick-walled and smooth and largely fill the oögonial cavity; they measure 16.3–21.2 μ, the mean 20.1 μ, in diameter.

The cardinal temperatures for growth are: minimum, 10° C; optimum, 30–32.5°; and maximum, 37.5°.

These observations on morphology and temperature-growth relations are in conformity with those reported by Tucker (1931).

PATHOGENICITY

Cuttings originally rooted in a mixture of sterile soil and sand were transplanted to 6-inch pots containing sterile potting soil, in the greenhouse. Pure cultures of the fungus, grown on a mixture of sterilized whole oats and wheat, were added to the soil of one lot of 50 plants; sterile oats and wheat, only, were added to another lot of 10 plants. After 14–16 days, a few plants in pots infested with the fungus ceased growing and assumed a yellowed appearance. Twenty days after inoculation, all the fungus-inoculated plants had stopped growth, had become yellow, and showed signs of wilting (fig. 3); stem lesions became visible 23 days after inoculation. Plants grown in pots which received only the sterile-grain mixture remained healthy and continued to grow. When the affected plants were removed from their pots and the soil was carefully washed away from the roots, lesions such as those observed on naturally infected plants were found in abundance. Isolations made from artificially infected stems and roots proved pathogenic upon reinoculation and produced symptoms indistinguishable from those caused by natural infection.

This same procedure was employed with plant material derived from seed sown in sterile soil; the results were similar to those already described.

Cultures of *Fusarium* spp., isolated together with *Phytophthora parasitica* from diseased material, were grown on the sterile-grain medium. This inoculum was added to sterile soil in 6-inch pots containing belladonna plants, according to the procedure outlined above. No visible symptoms of disease were observed after one month. Plants receiving this treatment were taken from their pots, and the soil was removed by washing in water; no

root necrosis was observed. It is concluded that the *Fusarium* spp. used in this test were not pathogenic to belladonna and did not contribute to the root-rot problem.

Belladonna plants have been observed to damp-off. The fungi concerned are usually *Pythium debaryanum* Hesse, *P. irregulare* Buis., and *P. ultimum* Trow, though occasionally *Phytophthora parasitica* has been isolated from

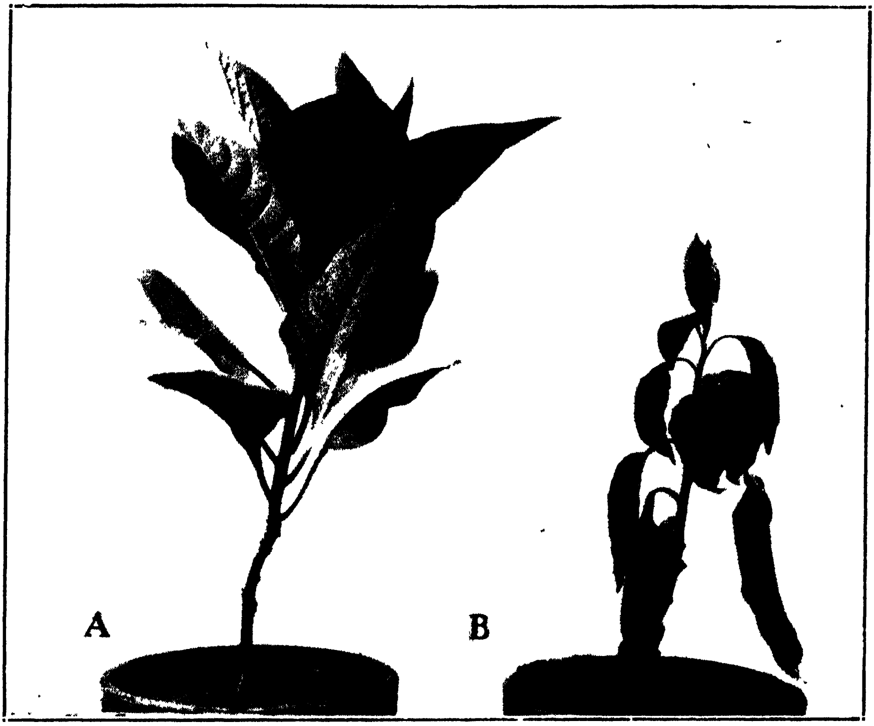


FIG. 3. Phytophthora rot of belladonna: A, noninoculated control; B, symptoms produced by *Phytophthora parasitica* 22 days after inoculation in the greenhouse.

such material. An experiment was devised to determine the ability of *P. parasitica* to cause damping-off of belladonna seedlings. A mixture of one-half sterilized soil and one-half fungus on whole-grain medium was placed in 10 sterile 6-inch pots; this mixture was covered by a thin layer of sterile soil. Five pots contained a mixture of one-half sterilized soil and one-half sterile grain. Fifty belladonna seeds were sown in each of the 15 pots. Four weeks later survival counts were made. In the 10 pots receiving the fungus, the surviving plants numbered: 5, 3, 0, 0, 2, 9, 6, 0, 1, and 4, respectively; in the 5 pots receiving sterile grain (control), the counts were: 37, 41, 26, 39, and 40, respectively.

The pathogenicity of the three *Pythium* spp. was likewise determined. The results showed greatest reduction in stand in the *P. ultimum* series and less reduction in the cases of *P. debaryanum* and *P. irregulare*.

Field observations seem to indicate that one of the principal methods of spread of the disease is through stem and leaf infections of adjoining plants, under conditions of warm air temperatures and high relative humidity. To test this, 49 potted plants were placed in a square group in a moist chamber. Bits of agar containing mycelium and sporangia of *Phytophthora parasitica* were placed in the axils of young shoots on 4 plants comprising the corners of the square border about the center plant. The chamber was atomized continuously with sterile distilled water; light was supplied during the normal daylight hours. Within 3 days infection of the young shoots and attached leaves was observed; the disease began to spread on the fourth and fifth days. Within 10 days the central mass of plants and all but 7 of the marginal plants were infected, the shoots becoming discolored and wilted, the leaves watersoaked and collapsed.

A similar experiment was arranged with 12 plants, in 3 rows of 4 pots each, the 2 center plants being inoculated as described above. After infection had occurred and the disease had begun to spread, atomization was suspended and all plants were sprayed with 2-2-50 bordeaux and a wetting agent, the plants remaining in the moist chamber. The disease was checked, and no further spread occurred over the next 7 days, when the experiment was concluded.

A similar experiment was set up using 14 plants. After the disease began to spread, 2 slightly infected plants were removed to another moist chamber which was wet but not atomized. The other 12 plants were treated exactly as in the previous test. Whereas the disease was checked by the application of bordeaux in the lot of 12 plants, the disease continued to spread in the plants which were not sprayed or atomized. Similar results were obtained by using 2–3–50 burgundy and 1.5 100 yellow cuprous oxide with wetting agent.

CONTROL

No experiments were conducted to determine the origin of infection in field plantings of belladonna, but infection is apparently accomplished in at least two ways: (1) through natural infection of healthy plants by the fungus previously established in the planting area and (2) through the introduction of diseased transplants. The last condition may be controlled through use of seedlings grown in sterile soil.

From field observations it is very evident that belladonna suffers severely from root-rot when grown on heavy soils. The disease also becomes very serious when an overhead irrigation system is employed. Plantings can be suc-

cessfully grown in light soils which are adequately drained and furrow-irrigated rather than sprinkled. The spread of the disease may be substantially reduced through abolishment of the overhead type of irrigation.

Where the disease is established and fungicidal control is necessary, 2–2–50 bordeaux, 2–3–50 burgundy, or 1.5–100 cuprous oxide, with a suitable wetting agent, may be employed to arrest aerial development of the disease.

Damping-off of belladonna may be satisfactorily controlled by seeding in sterile soil, fumigated either with carbon disulfide or with chloropicrin, or steam-pasteurized or autoclaved; sterile pots or flats should also be used. In watering, care should be exercised to avoid splashing water and soil from adjacent unsterilized plant containers. Preliminary investigations in which cuprous oxide, ethyl mercury phosphate, and tetrachloro-parabenzoquinone were used as seed protectants, were rather unsatisfactory, none of these materials effecting adequate control of damping-off.

SUMMARY

Phytophthora rot of belladonna (*Atropa belladonna* L.), occurring in California and affecting roots, crowns, stems, and leaves, is described. This is apparently the first detailed account of a Phytophthora rot of this host in the United States.

The causal organism has been identified as *Phytophthora parasitica* Dastur. The morphology of the fungus is typical of the species. The cardinal temperatures for growth are: minimum, 10° C; optimum 30° to 32.5°; and maximum, 37.5°. The pathogenicity of the fungus to mature and seedling plants has been established.

Control of the disease may be afforded by planting on light, well-drained soils and by the use of the furrow method of irrigation; overhead irrigation should be avoided. Control of the spread of the disease may be accomplished through abolishment of the overhead system of irrigation and the application of bordeaux, burgundy, or cuprous oxide with a suitable wetting agent.

The ability of *Phytophthora parasitica* and of *Pythium debaryanum* Hesse, *P. irregulare* Buis., and *P. ultimum* Trow to cause damping-off of belladonna is likewise described, and the pathogenicity of the fungi is established. Damping-off may be controlled by seeding in sterile soil in sterilized containers. Three materials used as seed-protectant dusts did not effectively control damping-off.

Literature Cited

Alcock, N. L. 1926. A preliminary note on a *Phytophthora* on *Atropa belladonna*. Pharm. Jour. **116:** 232.

Barker, B. T. P. 1917–1918. Diseases of plants and their treatment. Bath and West and South. Counties Soc. Jour. V. **12:** 189–193.

MacMillan, H. G. 1941. Some diseases of drug plants and herbs observed in southern California. Plant Dis. Reporter **25:** 443–445. (Mimeo.)

McCormick, Florence A. 1925. Perithecia of *Thielavia basicola* Zopf in culture and the stimulation of their production by extracts from other fungi. Conn. Exp. Sta. Bull. 269: 537–554.

Middleton, John T. 1941. Some diseases of belladonna in California and their control. Plant Dis. Reporter **25:** 513–514. (Mimeo.)

Parisi, Rosa. 1921. Di alcuni parassiti delle piante medicinale e da essenze. Boll. Orto. Bot. Napoli **6:** 285–296.

Tucker, C. M. 1931. Taxonomy of the genus *Phytophthora* de Bary. Mo. Exp. Sta. Res. Bull. 153: 1–208.

Westerdijk, Johanna, & van Luijk, A. 1920. *Phytophthora erythroseptica* Peth. als parasit von *Atropa belladonna*. Phytopath. Lab. "Willie Commelin Scholten," Meded. **4:** 31–32.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 252–260 MAY, 1943

THE MORPHOLOGICAL NATURE OF THE PHOTOSYNTHETIC ORGANS OF ORCHYLLIUM ENDRESII AS INDICATED BY THEIR VASCULAR STRUCTURE[1]

W. G. McINTYRE AND M. A. CHRYSLER

In spite of the notoriety attained by the "bladders" of the genus *Utricularia*, the morphological nature of the various organs remains unsettled. The aquatic habit appears to have brought about specialization accompanied by reduction. For this reason a mere inspection of the organs and even a comparison of organs in the different genera has led to sharp disagreement. This is illustrated by the selected references which follow.

Schimper (1882) reported his studies on *Utricularia cornuta*, a North American species found along the edges of swamps or on hummocks in moist places. He regarded the underground portions of this plant as branches of the main stem. Certain minute green blade-like organs arising from slender subterranean branches he considered to be of caulome nature.

Schenck (1887) appears to have been the first to have access to a species in which vascular tissues are fairly well developed. He described and presented good figures of the structure of the various organs in *U. montana*, an epiphytic species from the West Indies. He obviously was not impressed by the concentric structure of the "Blattstiel" nor its resemblance to the inflorescence axis, but assumed that the blade-shaped organs are leaves.

Ridley (1888), while describing a specimen of *U. bryophylla*, a small terrestrial species from South Africa, held that the leaf-like organs are of caulome nature because some become narrow toward the tip and continue as bladder-bearing branches.

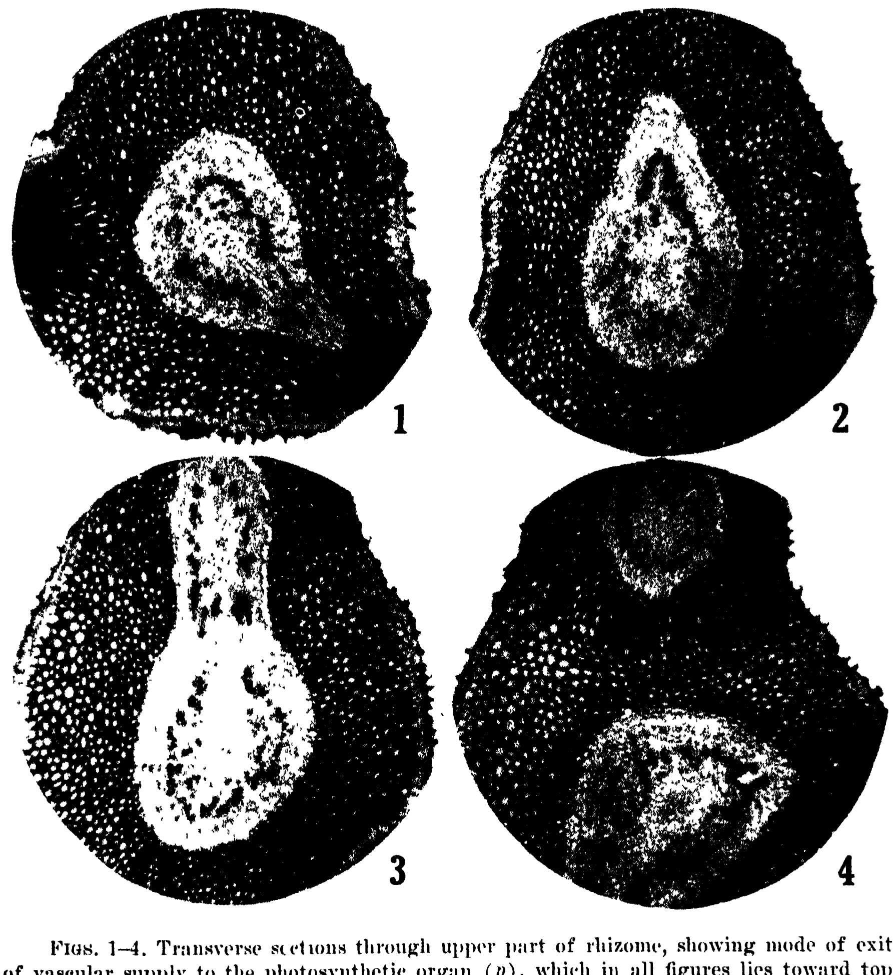
From a study of the South American genus *Genlisea* and several small terrestrial utricularias, Goebel (1898) concluded that all of the lateral organs are modified leaves, that is, all the organs which function as roots and stems are derived from leaves which have become first tubular and then solid branching structures.

In the present study an attempt is made to use the criterion of anatomical structure as exhibited in the Costa Rican species *Orchyllium Endresii* (Rchb. f.) Barnhart, suitably preserved material of which was secured by the second writer in the summer of 1940. Sections were prepared by paraffin and celloidin methods, serial sections being used when desirable. Crystal violet followed by erythrosin was found valuable for differentiating the slightly lignified vessels.

[1] Publication of Bureau of Biological Research, Rutgers University.

In contrast to many members of the family this plant is essentially terrestrial, growing in moss on fallen logs in wet forest, also in peaty matter bearing liverworts and lichens at the surface of crevices in steep banks. As might be expected, the vascular tissues are much better developed than is the case in aquatic members of the family.

The slender infloresecence axis has a height up to 35 cm. and bears from



FIGS. 1–4. Transverse sections through upper part of rhizome, showing mode of exit of vascular supply to the photosynthetic organ (*p*), which in all figures lies toward top of page. Figure 1 is the lowermost section. All × 25. FIG. 1. At lower right hand, early stage in exit of trace to a tuber-bearing branch. At top a slight bulge in xylem indicates beginning of trace supplying *p*. FIG. 2. About 100 μ above level of fig. 1, trace supplying *p* is diverging from stele of rhizome. FIG. 3. About 100 μ above level of fig. 2, trace supplaying *p* is beginning to assume circular outline. FIG. 4. About 100 μ above level of fig. 3, trace supplying *p* shows circular outline. At lower left, the trace of another *p* is leaving stele.

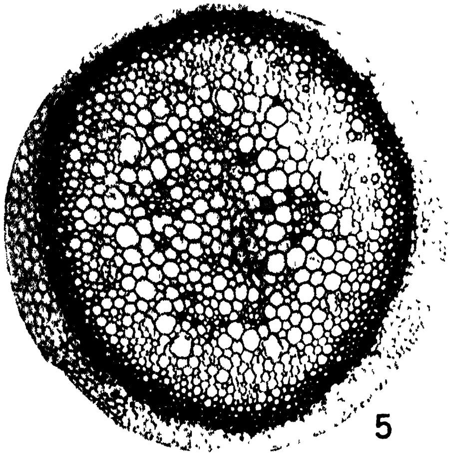
one to five flowers. The large size of the latter (30–40 mm. in width) and their orchid-like appearance as well as the almost epiphytic habit of the plant suggested the name *Orchyllium* to Barnhart (1916) when he segregated the genus from *Utricularia*. Scattered along the axis are several simple lanceolate bracts and at the base of each pedicel are a bract and a pair of bracteoles. The axis forms a vertical extension of the short subterranean stem, which has the appearance of being much condensed. From this stem arise organs of four kinds: (1) the inflorescence axis already mentioned; (2) one or two vertically disposed photosynthetic organs—the so-called leaves; (3) several delicate horizontal or downwardly directed branches bearing minute but perfect "bladders" and functioning as absorbing organs in default of true roots; (4) several stouter branches each of which swells into a translucent tuber 5–8 mm. in diameter and then continues like (3).

The blade of each "leaf" has a length of 40–60 mm. and width of 10–20 mm., is from lanceolate to ovate in shape with the tip acute and the base tapering into the stalk which may have a length of 30–60 mm. There is a pronounced midrib, from which at an acute angle diverge veins which anastomose with one another. The whole organ is inclined to be stiff.

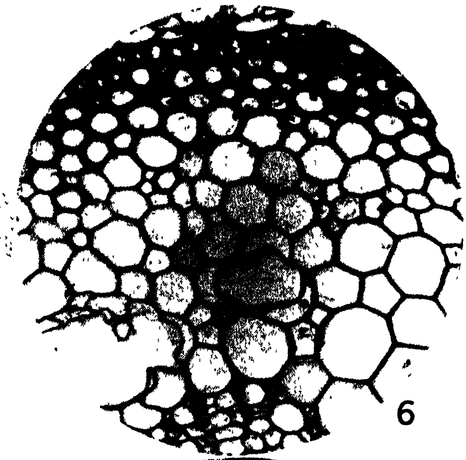
It will now be in place to examine the internal structure of the chief organs. The most conspicuous feature of the rhizome is the wide and thick-walled middle layer of the cortex (figs. 1–4), bounded inwardly and outwardly by narrow layers of thin-walled cells. The epidermis is studded with sac-shaped absorbing hairs. An endodermis is hard to demonstrate, but cells showing a Caspary's band when treated with safranin and fast green form a much interrupted ring bounding the central cylinder. In the stele it will be noticed that the vessels are distributed through an annular zone among thin-walled cells. All of them are narrow (15–30 μ) with spiral or reticulate thickening. Groups of delicate phloem cells (unstained in figures 1–4 but clearly shown in figure 6 representing the inflorescence axis) are scattered through the stele without reference to the xylem. Toward the base of the rhizome the vessels are more or less grouped into bundles with which phloem groups are occasionally associated. The endodermis moreover is readily identified in this region. These observations appear to indicate that the more scattered condition of the vessels and discontinuous nature of the endodermis are due to dilation of the stele.

Explanation of figures 5–10

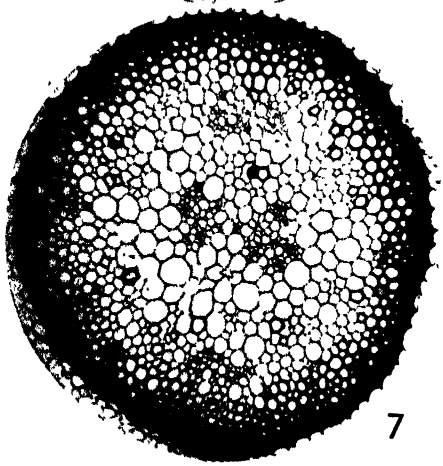
FIG. 5. Transverse section through inflorescence axis. ×45. FIG. 6. Part of same section. ×175. Six vessels and several phloem groups are shown. FIG. 7. Trans sec. through midrib of photosynthetic organ. ×100. FIG. 8. Part of same section. ×235. Eight vessels, also large and small phloem groups, are shown. FIG. 9. Blade of photosynthetic organ, showing at left a branch of the stele, at lower right a stoma. ×105. FIG. 10. Inflorescence axis at level of exit of the three traces which supply one of the bracts. ×55.



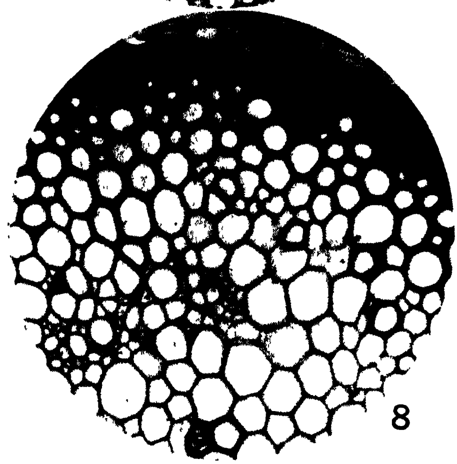
5



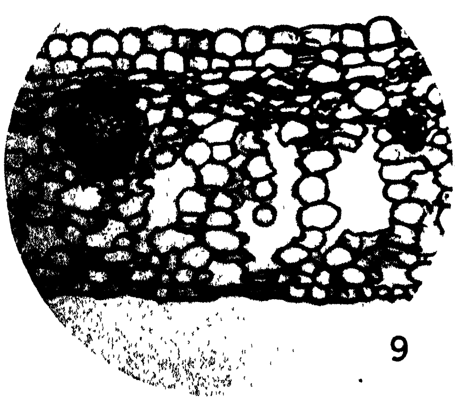
6



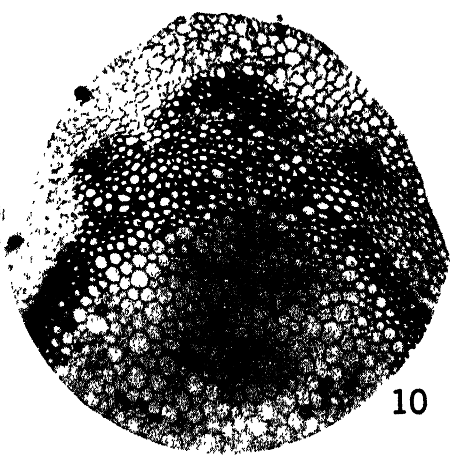
7



8



9



10

As the rhizome passes into the inflorescence axis (fig. 5) the cortex loses its thick-walled character and consists of four or five layers of parenchyma cells liberally provided with intercellular spaces which are associated with stomata. The stele takes on a new feature, namely, a thick-walled zone about five cells in thickness and lying immediately beneath a clearly marked endodermis. This mechanical layer shades off into the pith. The xylem (fig. 6) continues the annular arrangement characteristic of the rhizome, but the vessels are much less numerous, while a few are to be found in the middle region of the stele; all are thin-walled and poorly lignified but show clearly when stained with crystal violet. The phloem groups are very numerous, some small ones occurring in the mechanical layer and extending quite to its outer edge while several large groups may be present in the middle region of the stele. Thus the vascular tissues of rhizome and inflorescence axis correspond while differing in detail. That the unusual arrangement of the vascular elements is characteristic of *Utricularia* sec. *Orchidoides* (= *Orchyllium* Barnh.) is indicated by Schenck's (1887) figure 5 of the inflorescence axis in *U. montana*. The situation of the vessels among thin-walled cells is a sign of reduction from a more or less continuous xylem cylinder, which reduction is carried so far in the aquatic species that xylem is scarcely discernible. The position of the phloem groups may be interpreted as an extension of the tendency to produce additional phloem groups seen in various members of Solanaceae, Convolvulaceae, and several other sympetalous families.

When we turn to the photosynthetic organs, figure 7 shows the appearance at the level of expansion from stalk to blade. Beneath the epidermis a cortex 4–5 cell layers in thickness is followed by a definite endodermis and a mechanical ring consisting of a few thick-walled layers shading off to the thin-walled cells of the axial ground tissue. This region shows very thin-walled isolated vessels in a peripheral zone, a few in a more central position, and larger or smaller groups of delicate phloem cells scattered through the ground tissue but in this organ rarely invading the mechanical layer, so far as our observations indicate. Several rather large phloem groups are apt to occur in the central region. Longitudinal sections show that the thickenings of the vessels are of the annular, spiral, and reticulate types, all very poorly lignified. Thus point by point the vascular tissues corrsepond in arrangement and structure with those found in the stele of the inflorescence axis. Surely it is just as proper to call the area enclosed by the endodermis a stele as in the two regions of the stem. Small portions of the stele are pinched off to supply the veins of the lamina; the largest of these have a nearly complete mechanical sheath surrounding a very poorly developed central xylem and three or four small peripheral phloem groups; smaller veins show dorsal and ventral mechanical areas, the former frequently being the smaller of the two, with the phloem groups persisting on the flanks. The strands hence resemble

steles rather than collateral bundles. The blade (fig. 9) presents the following layers: (1) an upper epidermis which may have a few glandular hairs of the type occurring on the rhizome; (2) four or five layers of nearly cubical cells, the inner ones containing chloroplasts and reminding one of poorly developed palisade; (3) a spongy layer occupying most of the thickness of the organ; (4) a lower epidermis with stomata of an unspecialized type and glandular hairs in larger numbers than on the upper surface. Obviously the blade would pass for a leaf were it not for the stelar nature of the vascular structures and the similarity of these to the ones found in the stem. It should be remarked that the dorsiventral structure of the blade need not enter into the argument, in view of the fact that the unquestioned flat branches of *Phyllocladus* bear far more stomata on the lower side and show a palisade toward the upper side. These features are to be regarded as strictly ecological.

Schenck's figure 11 (1887) representing the "mid-rib of the leaf" of *U. montana* resembles our figure 7 except that in the former the vessels are somewhat less evenly distributed. Hovelacque (1887) has undertaken to interpret Schenck's figure 6, representing a runner, as showing an arc-formed grouping of the vessels, hence the runner is a phyllome, not a caulome as Schenck held. Realizing that all evidence of dorsiventrality should be considered, and that some of the small vessels may easily be overlooked, we have outlined under high magnification with camera lucida the set of vessels occurring in the section photographed in figure 7. Thirty-four undoubted vessels were found, all but four of them making up an interrupted ring-formed zone, not in any way suggesting an arc. The phloem in our figure looks a trifle suspicious, showing four large groups more or less on an axis running at right angles to the width of the blade, but the illusion is dispelled by a glance at other sections, which show that the phloem groups anastomose so as to present various arrangements. Hovelacque's argument hence appears to have no application to *O. Endresii*, which is probably a more primitive plant than *U. montana* because the former has a better developed primary axis and simpler branches.

Additional light on the morphological status of the photosynthetic organ is afforded by examination of the region where it branches off from the rhizome. Figures 1–4 represent sections selected from a series taken through the stem. Reference is made to the legend, which sufficiently indicates that the vascular system of the so-called leaf arises as a concentric group, not a collateral one; that is, we are here dealing with a flattened branch, not a leaf. It is instructive to compare these sections with those cut from an inflorescence axis at the level of origin of one of the bracts. In spite of its small size the bract is supplied by three vascular bundles, arising separately from the stele of the axis (fig. 10), the median bundle being larger than the laterals. It

will be recalled that this is the typical mode of origin of the vascular supply of a leaf. The contrast between figures 10 and 3 is sufficiently striking. In sections through a bract the median bundle is represented by 4–6 vessels arranged in a broken row parallel with the surface of the bract; applied abaxially to these several minute groups of phloem; finally a conspicuous island of mechanical fibres—essentially a collateral bundle.

Plainly *Orchyllium* has not entirely lost the power of producing leaves, and these are unmistakable when they do occur. It would naturally be gratifying to find a leaf or bract subtending a photosynthetic organ, comparable with the bract occurring at the base of each cladophyll in *Ruscus*, but nothing of the kind appears to be present. This seems to be one of the features of reduction in this very specialized subterranean organ. It will be recalled that the bract which usually subtends each flower of a raceme is typically absent in Cruciferae.

Petioles showing a stele-like bundle are of course known in different groups of plants; for example, several species of the fern genus *Gleichenia* show a concentric arrangement of xylem and phloem and even a pith area in certain regions of the leaf axis; but this represents a pseudostele, formed by fusion of the edges of a C-shaped leaf trace, as was pointed out by Jeffrey and others. Likewise the concentric structure seen in the petiolar bundle of some species of *Primula* has been shown by Gwynne-Vaughan (1897) to be the result of the same process as occurs in *Gleichenia*. In *Orchyllium*, however, the concentric trace supplying the photosynthetic organ arises in a quite different manner, as we have shown.

In view of the evidence derived from internal structure, the inference appears inescapable that in *Orchyllium* the photosynthetic organs are not leaves but flattened stems of limited growth, hence the name cladode is applicable. Naturally the early students of the bladderworts interpreted the organs by comparing the external form in various species and genera. Even Schenck, who made a careful study of *U. montana*, apparently failed to perceive the implication of the vascular structures exhibited in this close relative of *O. Endresii*, for without comment he called the green organs "leaves." But this was in 1887. Meanwhile it has come to be realized that the vascular parts of a plant are less liable to modification by reason of changes in the environment than is the external form. Hence the vascular anatomy furnishes one of the most reliable criteria for establishing morphological concepts and for determining relationships. Goebel was an earnest student of the group, but even in his later contributions paid scant attention to vascular structures. He reached the somewhat disconcerting conclusion that in *Utricularia* and its allies: "kurtz es ist das gewöhnliche Schema der Organbildung hier ganz über den Haufen geworfen." (Goebel 1898, p. 446). His trans-

lators have rendered the last phrase as "jumbled," which probably expresses the meaning rather mildly.

The anatomical evidence furnished by such terrestrial species as *O. Endresii* and *U. montana* is so consistent that it becomes probable that the small green blade-like organs arising from the creeping stem of *U. cornuta* are also of caulome nature, as was suggested by Schimper (1882). Barnhart's study of the family led him on the basis of external features such as bracts to place his new genus *Orchyllium* next to Rafinesque's genus *Stomoisia*, which includes the former *U. cornuta* and other species. These near-aquatics naturally have practically no vascular tissues, but have in all probability been derived from terrestrial plants, so that the systematic position of *Stomoisia* and other segregates may be significant.

We are not prepared however to extend the cladode theory to all members of the family. The vascular structures in the different genera show considerable differences. Thus Van Tieghem (1869) reported that in *U. vulgaris* the stele has a narrow central vessel surrounded by elongated cells containing a granular liquid. This is a reduced condition of the xylem which is shown by other aquatics, e.g., *Elodea.* Dangeard and Barbé (1887) observed in *Pinguicula* the condition which they called polystely and compared with the similar condition in *Primula Auricula.* Merl (1915) furnished an account of the anatomy of several species of *Genlisea*, finding in all a sclerenchymatous ring surrounding a circular series of phloem groups, with vessels distributed through the pith. It will be noticed that none of these plants has an arrangement of vascular tissues like that described by Schenck (1887) and the present writers. In view of this diversity in the vascular tissues, it would be unwarranted to claim that cladodes occur throughout the family. *Pinguicula*, *Genlisea*, and *Utricularia* are so different in various respects that the family must have had a long history which is at present unknown. Goebel may well be correct in regarding all the organs of *Genlisea* as modified leaves, but the observations presented in this paper strongly support the earlier view of Schimper and others that the flattened organs in *Utricularia*, *sensu lato*, are of the nature of branches.

SUMMARY

The problem of the morphological nature of the photosynthetic organs in *Utricularia* is approached from the point of view of vascular structure in the terrestrial tropical *Orchyllium Endresii.* In this species the vascular tissues are fairly well developed, and so-called leaves are conspicuous organs.

The stele of the underground stem presents a ring-formed group of vessels interspersed in much parenchyma, and numerous small groups of phloem cells scattered through the stele. The inflorescence axis has a similar structure, with vessels more scattered. The stalk of the "leaf" is constructed

almost exactly like the preceding organ, and its vascular supply arises from the stele of the stem as a concentric rather than collateral organ.

The only organs with leaf structure are the bracts on the inflorescence axis. The vascular supply of a bract consists of a median and two smaller lateral bundles arising separately from the stele of the inflorescence axis.

These observations indicate that the so-called leaf of *Orchyllium* is to be regarded as a specialized branch or cladode. It is suggested that cladodes may be present in aquatic members of the family in which vascular tissues are reduced to the vanishing point.

DEPARTMENT OF BOTANY, RUTGERS UNIVERSITY
NEW BRUNSWICK, NEW JERSEY

Literature Cited

Barnhart, J. H. 1916. Segregation of genera in Lentibulariaceae. Mem. N. Y. Bot. Gard. **6**: 39–64.

Dangeard, P. A., & Barbé, C. 1887. La polystélie dans le genre *Pinguicula*. Bull. Soc. Bot. France **34**: 307–309.

Goebel, K. von. 1898. Organographie der Pflanzen.

Gwynne-Vaughan, D. T. 1897. On polystely in the genus *Primula*. Ann. Bot. **11**: 307–325.

Hovelacque, M. 1887. Structure et valeur morphologique des cordons souterrains de l'*Utricularia montana*. Compt. Rend. Acad. Sci. **105**: 692–695.

Merl, E. M. 1915. Beiträge zur Kenntnis der Utricularien und Genliseen. Flora **108**: 127–200.

Ridley, H. N. 1888. On the foliar organs of a new species of *Utricularia* from St. Thomas, West Africa. Ann. Bot. **2**: 305–307.

Schenck, H. 1887. Beiträge zur Kenntnis der Utricularien. Jahrb. Wiss. Bot. **18**: 218–235.

Schimper, A. F. W. 1882. Notizen über insectenfressende Pflanzen. III. *Utricularia cornuta*. Bot. Zeit. **40**: 241–248.

Van Tieghem, Ph. 1869. Anatomie de l'utriculaire commune. Ann. Sci. Nat. V. **10**: 54–58.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 261–264 MAY, 1943

POLYPLOIDY IN SEDUM PULCHELLUM—II. STOMATAL SIZE AND FREQUENCY[1]

HARRIET E. SMITH

Within recent years it has been found that in many groups of plants polyploids can be distinguished from diploids by comparing the size and frequency of stomata. An increase in chromosome number is accompanied by an increase in stomatal size and a decrease in stomatal frequency in *Zea* (Randolph 1932, 1935), *Tradescantia* (Sax & Sax 1937), *Coffea* (Franco 1939), and other genera. It has been suggested that such a relationship between stomata and chromosome number would aid in detecting polyploid races in herbarium material, and stomatal size and frequency have actually been so used as criteria for polyploidy (Babcock & Stebbins 1938; Stebbins 1939; Sax & Sax 1937). This also offers a ready clue toward determining polyploid races of living plants.

To ascertain the size and frequency of stomata in *Sedum pulchellum*, studies were made on the diploid ($2n=22$), tetraploid ($2n=44$), and hexaploid ($2n=66$) races. Counts were made on the diploid for 19 plants from 16 locations, on the tetraploid for 19 plants from 12 locations, and on the hexaploid for 12 plants from 3 locations.[2] The chromosome counts were made by J. T. Baldwin, Jr., from aceto-carmine smears of roots and leaves, and some from Nawaschin-fixed, crystal-violet-stained sections of roots.

Since environmental conditions and position of leaf on the plant have been found to affect the size and distribution of stomata in some species (Franco 1939; Hirano 1931), the plants studied were grown under uniform conditions and counts were made only from basal juvenile leaves of plants at a uniform stage of development. Although preliminary observations indicated that stomatal size and frequency do not vary appreciably in the same leaf in *Sedum pulchellum*, an attempt was made always to take the count from the middle portion of the lower epidermis of the leaf.

Lloyd's method (Lloyd 1908) for measuring stomata was used: the lower epidermis was stripped from the leaf and fixed at once in absolute alcohol (Lloyd found no measurable shrinkage of stomatal size under this treatment). Measurements of five open stomata on each leaf were made with an eyepiece micrometer, a Spencer microscope with a $10\times$ ocular and $44\times$ objective being used; stomatal counts were made with a $10\times$ ocular and

[1] Papers from the Department of Botany of the University of Michigan, No. 816.

[2] Collections were made by: J. T. Baldwin, Jr., Jean M. Campbell, L. M. Dickerson, R. M. Harper, A. M. Harvill, Milton Hopkins, D. W. Moore, H. T. Shacklette, J. A. Steyermark, Mary E. Wharton.

$10\times$ objective; the total number of stomata per microscopic field was determined and the statistical comparison of races was based on the number of stomata per field. The numbers were converted later to number of stomata per square millimeter.

Individual plants in each race vary so greatly morphologically that it would be hazardous to judge the degree of polyploidy by the general appearance of a single plant; however, when large numbers of plants of different races are studied, racial differences can be discovered. In the diploid, the juvenile leaves are small and densely crowded, giving the plant a compact appearance. In the tetraploid, leaves are slightly darker in color, larger, and not so densely crowded. The tetraploids appear to be healthiest and most vigorous. Hexaploid leaves are broadest, and in length are intermediate between those of the diploid and the tetraploid (fig. 1). The hexaploid has

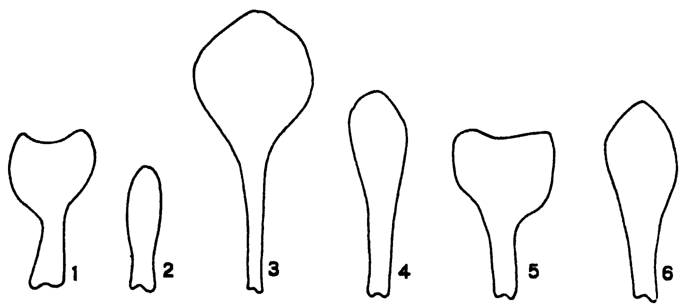


FIG. 1. Primary and secondary juvenile leaves of *Sedum pulchellum*. 1. Primary leaf of diploid, $2n=22$. 2. Secondary leaf of diploid. 3. Primary leaf of tetraploid, $2n=44$. 4. Secondary leaf of tetraploid. 5. Primary leaf of hexaploid, $2n=66$. 6. Secondary leaf of hexaploid. All $\times 2$.

fewer but longer stems than the tetraploid, giving the hexaploid a more diffuse appearance. Measurements of mature leaves are being analysed statistically and will be published later. Diploids mature and flower earlier than the other two races. The three races occupy different geographical regions (Baldwin 1942).

Stomatal size was found to vary directly with chromosome number, and stomatal frequency inversely with chromosome number (table 1). The differences in the means of the different races all give very high values of t,

TABLE 1. *Stomatal Size and Frequency in Sedum pulchellum*

Chromosome number	Number of plants	Mean stomatal size in μ	Mean number of stomata per field	Mean number of stomata per sq. mm.
$2n=22$	19	269 ± 3	$83.3\ \pm2.125$	697
$2n=44$	19	457 ± 8	$53.6\ \pm1.005$	449
$2n=66$	12	575 ± 6	42.75 ± 1.5	358

the smallest being $t=6$; therefore these differences are statistically highly significant.

It must be emphasized that environmental conditions and other factors as well as chromosome number can strongly influence the frequency of stomata. In an attempt to learn how polyploidy exerts effect, therefore, it should be worth while to study the influence of environment upon the size and distribution of stomata. Yapp (1912), Salisbury (1927), and Maximov (1929) have found stomatal frequency to be correlated negatively with water supply: sun leaves have more stomata per unit area than shade leaves; plants grown under dry conditions have more stomata than those under humid conditions; upper leaves of many herbs and shrubs have more stomata than lower leaves, the upper leaves being farther from the source of water supply. Yapp and Salisbury consider high stomatal frequency to be a xeromorphic character. Maximov and Salisbury have found that in plants having more stomata on the upper leaves than on the lower ones, the upper leaves have a greater osmotic pressure than the lower ones. Thus high stomatal frequency appears to be correlated with high osmotic pressure. Yapp and Maximov in discussing the cause of high stomatal frequency in the upper leaves of a plant advance the theory that high stomatal frequency is actually caused by high osmotic pressure in the leaf while the leaf is developing and expanding. Although in this study on *Sedum* no attempt has been made as yet to determine osmotic pressures of the different chromosome races, Becker (1931), working with mosses, found osmotic pressure to be inversely proportional to chromosome number. If this should be found to be a general characteristic of polyploidy, then the high stomatal frequencies of the diploids and low frequencies of the hexaploids would be correlated with differences in osmotic pressure and would, accordingly, agree with Yapp's theory.

The ecological significance of stomatal size and frequency is somewhat uncertain. Salisbury (1927), in his study on the ecological significance of stomatal frequency, concludes that since the correlation between number of stomata and humidity is negative, stomatal frequency has no adaptational significance in relation to transpiration or assimilation. Yapp (1912), on purely theoretical grounds, concludes that the transpiration rate through the smaller but more numerous stomata of xeromorphic leaves should not be much greater than that through the larger but fewer stomata of less xeromorphic leaves, but Smith (1941) has found a significant positive correlation between stomatal frequency and transpiration in *Phaseolus vulgaris*.

SUMMARY

Stomatal size and frequency in juvenile leaves of three races of *Sedum pulchellum* were determined: stomatal frequency varies inversely with chromosome number; stomatal size varies directly with chromosome number.

When grown under constant environmental conditions, the three races differ morphologically, but there is also great variation within each race.

A possible relationship between chromosome number, osmotic pressure, and stomatal size and frequency is suggested.

The ecological significance of stomatal size and frequency is uncertain.

DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN
ANN ARBOR, MICHIGAN

Literature Cited

Babcock, E. B. & Stebbins, G. L., Jr. 1938. The American species of *Crepis*, their interrelationships and distribution as affected by polyploidy and apomixis. Carnegie Inst. Wash. Publ. 504: 1–100.

Baldwin, J. T., Jr. 1942. Polyploidy in *Sedum pulchellum*—I. Cytogeography. Bull. Torrey Club **70**: 26–33.

Becker, G. 1931. Experimentelle Analyse der Genom- und Plasmonwirkung bei Moosen. III. Osmotischer Wert heteroploider Pflanzen. Zeits. Ind. Abstamm. u. Vererb.-Lehre **60**: 17–38.

Franco, C. M. 1939. Relation between chromosome number and stomata in *Coffea*. Bot. Gaz. **100**: 817–827.

Hirano, E. 1931. Relative abundance of stomata in *Citrus* and some related genera. Bot. Gaz. **92**: 296–310.

Lloyd, F. E. 1908. The physiology of stomata. Carnegie Inst. Wash. Publ. **82**: 1–142.

Maximov, N. A. 1929. The plant in relation to water. George Allen and Unwin Ltd. 1–451.

Randolph, L. F. 1932. Some effects of high temperature on polyploidy and other variations in maize. Proc. Nat. Acad. **18**: 222–229.

————. 1935. Cytogenetics of tetraploid maize. Jour. Agr. Res. **50**: 591–605.

Salisbury, E. J. 1927. On the causes and ecological significance of stomatal frequency with special reference to the woodland flora. Phil. Trans. Roy. Soc. B. **216**: 1–65.

Sax, K. & Sax, H. J. 1937. Stomata size and distribution in diploid and polyploid plants. Jour. Arnold Arb. **18**: 164–172.

Smith, Hugh B. 1941. Variation and correlation of stomatal frequency and transpiration rate in *Phaseolus vulgaris*. Am. Jour. Bot. **28**: 722–725.

Stebbins, G. L., Jr. 1939. Notes on some systematic relationships in the genus *Paeonia*. Univ. Calif. Publ. Bot. **19**: 245–266.

Yapp, R. H. 1912. *Ulmaria palustris* and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. **26**: 815–871.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 3, pp. 265–274 MAY, 1943

THE NORTH AMERICAN SPECIES OF ERIGERON CENTERING ABOUT E. SPECIOSUS (LINDL.) DC. AND E. GLABELLUS NUTT.

ARTHUR CRONQUIST

In the course of preparing a revision of the North American species of *Erigeron*, I think it advisable to place the following treatment of some western species on record, in order that certain names and combinations may be made available for use. Citation of specimens, and discussions of phylogeny and evolutionary trends, are reserved for inclusion in a later more extensive work.

This study is intended to include the biennial and perennial North American species of *Erigeron* that have double pappus and erect stems with broad cauline leaves, exclusive of *E. philadelphicus* L. and its immediate relatives. Roughly, it includes the sections *Macranthi*, *Glabelli*, and *Asperi* of Dr. Rydberg's treatments. These forms constitute an entirely natural group.

As in many genera of the *Compositae*, complete morphologic discontinuity between species does not always exist. Intermediates can be found between forms that by any reasonable taxonomic system must be recognized as valid species. Those units which are comparatively distinct from other units, and whose subunits, if any, all share some common character or characters not found in closely related units, have been recognized as species. Geographic distribution of each of the groups recognized as a species is fairly continuous.

Following immediately on the question of specific criteria is the problem of intraspecific units. I wish to place on record here my concept of these.

Subspecies: An intraspecific unit, more or less genetically continuous through time because of a tendency for its individuals to breed largely among themselves, which occupies a largely distinct range of its own, and intergrades with other units where their ranges meet; or, a group of varieties that are more closely related to each other than to other varieties of the species.

Variety: An intraspecific unit, more or less genetically continuous through time because of a tendency for its individuals to breed largely among themselves, which shares a large part of its range with similar units, or which occurs anywhere within the range of a given species or subspecies.

Form: A minor intraspecific unit which occurs sporadically through part or all of the range of a species or major intraspecific unit, does not occupy any sizeable area to the exclusion of other individuals of the species, and

whose individuals show no obvious tendency, other than that induced solely by proximity, to breed largely among themselves.

In any monographic work, the nomenclaturally typical unit of a species should receive the conventional varietal or subspecific epithet if there are any major units within the species. It is not desirable, however, to grant the typical unit an epithet as a *forma*, unless, as is not usually done, all of the formae of that species are treated and named.

It is my conception that any real subspecies or variety will probably have some habitat preferences or peculiarities of its own developed to a greater or lesser degree, so that it is not necessary to grant subspecific status to ecotypes which are not geographically segregated.

The criteria used in this treatment are mostly external and superficial, such as the width of the phyllaries, size and distribution of the leaves, and pubescence. Width of the phyllaries, hitherto apparently almost totally disregarded, seems to be of considerable importance. Each of the species varies about its own mean, with the extremes commonly overlapping the extremes of certain other species. The width of the phyllaries is particularly helpful in distinguishing doubtful forms of *E. superbus* from *E. speciosus*, and *E. formosissimus* from *E. subtrinervis*. Associated with phyllary width is the degree of looseness of the tips. *E. superbus*, *E. formosissimus*, and *E. glabellus* are notable for the comparatively close tips of the phyllaries in mature heads, while *E. speciosus* and *E. subtrinervis* are notable for the very loose tips of the phyllaries.

Distribution and relative size of the leaves are very helpful. With the exception of *E. superbus*, the group may be divided into those forms in which the basal leaves are largest and the upper ones progressively and conspicuously reduced, and those in which the middle leaves are as large as or somewhat larger than the basal ones, with the upper ones only gradually reduced.

Type and distribution of pubescence are generally helpful, each unit here recognized having its own characteristic vesture. Number and width of ligules are occasionally helpful, as are height of the plant and persistence or deciduousness of the basal leaves. Size and number of heads, and shape of the inflorescence have only very limited usefulness, being too variable in most of the species to be of much help. Length and color of the ligules, and character of the short outer pappus seem to be wholly unreliable in this group of species. More technical characters of the achenes and disc corollas are in general too uniform to be of much value in the group.

About 2500 sheets, from 15 herbaria, have been assembled for this study. I wish to thank the curators for their kindness in loaning specimens. Grateful acknowledgement of assistance is made to Dr. Ray J. Davis, who has spared no effort to assemble the necessary materials and has given continued

advice and encouragement, to Dr. Bassett Maguire, who has been most generous in providing access to necessary literature, and to my wife, Mabel Allred Cronquist, who has assisted and encouraged the study in various ways.

KEY TO THE SPECIES

1. Stem leaves glabrous or glandular, not even ciliate on the margins, comparatively few and little if at all longer than the internodes ... 1. *E. superbus*
1. Stem leaves either obviously pubescent or at least ciliate on the margins, sometimes also glandular, often numerous and longer than the internodes.
    2. Plant rather equably leafy, the upper stem leaves gradually rather than conspicuously reduced, the middle stem leaves commonly larger than the lowermost ones.
        3. Upper and middle stem leaves glabrous or nearly so except for the ciliate margins; stem glabrous below the inflorescence or bearing a few scattered hairs ... 2. *E. speciosus*
        3. Upper and middle stem leaves obviously hairy or glandular or both, or the stem conspicuously pubescent with long spreading hairs.
            4. Leaves glandular or glandular-scabrous, sometimes also sparsely long-hairy.
                5. Leaves without long eglandular hairs except for the ciliate margins and occasional long hairs along the midribs; stem pubescent above with stiff spreading hairs; plants of Arizona and New Mexico ... 3. *E. platyphyllus*
                5. Leaves and stem sparsely pubescent with long, soft, flexuous hairs; plants of southwestern Wyoming to central Utah ... 4. *E. uintahensis*
            4. Leaves hairy, not glandular or the uppermost ones but slightly glandular ... 5. *E. subtrinervis*
    2. Plant rather inequably leafy, the upper leaves conspicuously reduced, the middle ones commonly smaller than the lowermost ones.
        3. Stem and involucre glandular or viscid, sometimes also hairy. ... 6. *E. formosissimus*
        3. Stem and involucre more or less hairy, not at all glandular or viscid ... 7. *E. glabellus*

TREATMENT OF THE SPECIES

1. Erigeron superbus Greene ex Rydb. Colo. Exp. Sta. Bull. 100: 351, 364. 1906. *E. apiculatus* Greene, Leafl. **2**: 217. 1912. *E. eldensis* Greene, Leafl. **2**: 196. 1912. *E. macranthus* subsp. *mirus* A. Nels. Proc. Biol. Soc. Wash. **17**: 178. 1904.

Perennial herbs arising from simple or slightly branched caudices, commonly bearing tufts of radical leaves at the ends of short rhizomes; stems 1 or several, 1.5–6 dm. high, glabrous below, glandular in the inflorescence; leaves more or less triple-nerved, few, commonly shorter than or barely exceeding the internodes, obtuse or acute, apiculate, entire or some, especially the lower, denticulate or crenulate, not ciliate on the margins, or the lowermost but slightly so toward the bases of the petioles; basal and lowermost cauline leaves glabrous, persistent, oblanceolate to oval, rather abruptly narrowed to winged petioles, the blade and petiole 3–15 cm. long and 10–33 mm. wide;[1] middle cauline leaves smaller than or equalling those below, lanceolate to oblong or ovate, glandular; heads mostly 1–7, rarely as many

[1] Here and elsewhere figures for width of leaf refer to maximum width of blade.

as 16, commonly cymose and borne on nearly naked peduncles, the discs 11–19 mm. wide and 6–10 mm. high; phyllaries in one or two equal series, glandular, occasionally with a few long hairs, the outer ones broad, mostly 0.8–1.3 mm. wide, acuminate, the tips appressed or a little loose; ligules comparatively few, mostly 40–80, 1–2 mm. wide and 12–20 mm. long, blue or rose-purple, rarely white; pappus double, the outer setulose and sometimes very scanty. Mountains; southern Wyoming, Colorado, Utah, New Mexico, and Arizona. Not common.

Erigeron superbus has sometimes been regarded as conspecific with *E. eximius* Greene, which was published several years before *E. superbus*. Through the kindness of Dr. Theodor Just, the type of *E. eximius* in the Greene herbarium at Notre Dame has been carefully checked and photographed. It is *E. formosissimus*, variety *viscidus*, with which *E. superbus* intergrades to some extent.

2. ERIGERON SPECIOSUS (Lindl.) DC. Prodr. **5**: 284. 1836.

Perennial herbs with more or less branched woody caudices; stem 1.5–8 dm. high, glabrous, or sometimes slightly hairy or glandular in the inflorescence, usually with a few hairs just under each head; leaves commonly but not always triple-nerved, entire but with ciliate margins, the cilia sometimes very few or present only along part of the margin, glabrous or sometimes with a few hairs along the main veins, the basal and lowermost cauline ones oblanceolate to broadly spatulate, narrowed to winged petioles, the blade and petiole mostly 5–15 cm. long and 4–20 mm. wide, usually deciduous or withered by flowering time; middle cauline leaves as large as the lower, or commonly larger, narrowly lanceolate or oblong to broadly ovate or oval, acute or sometimes obtuse, apiculate, sessile, 3–11 cm. long and 5–28 mm. wide; upper leaves usually not markedly reduced, narrowly lanceolate to broadly ovate, occasionally minutely glandular; heads 1–13, cymose or cymose-paniculate, the discs 6–13 mm. high and 11–22 mm. broad; phyllaries in about two equal series, glandular and sometimes with a few long hairs, the outer ones mostly 0.4–0.8 mm. wide, acuminate or attenuate, the tips loose; ligules numerous, about 75–150, about 1 mm. wide, 9–18 mm. long, blue, rarely white; pappus double, the outer commonly setulose. Mountains and woodlands; southern British Columbia and Alberta to northern Oregon, eastward and southward to Montana, western South Dakota, New Mexico, and Arizona; an isolated station in the Sierra San Pedro Martir, Baja California.

1. Uppermost leaves lanceolate; phyllaries commonly with a few hairs . . . a. var. *typicus*
1. Uppermost leaves ovate; phyllaries without hairs . . . b. var. *macranthus*

2a. **Erigeron speciosus** (Lindl.) DC. var. **typicus,** Cronquist var. nov. *Stenactis speciosa* Lindl. Bot. Reg. **17**: *pl. 1577*. 1833. *E. speciosus* DC. Prodr. **5**: 284, as to type. 1836. *E. salicinus* Rydb. Bull. Torrey Club **32**: 125. 1905.

Stem sometimes slightly hairy above; uppermost leaves lanceolate, often strongly ciliate all around, sometimes with a few hairs on the surface; phyl-

laries commonly with a few hairs. Range of the species, but most common in British Columbia, Washington, Oregon, and northern Idaho.

2b. **Erigeron speciosus** (Lindl.) DC. var. **macranthus** (Nutt.) Cronquist, comb. nov. *E. macranthus* Nutt. Trans. Am. Phil. Soc. II. **7**: 310. 1841. *E. Vreelandii* Rydb. Bull. Torrey Club **32**: 125. 1905. (See note under *E. platyphyllus* Greene.) *E. eucephaloides* Greene, Leafl. **2**: 216. 1912. *E. leiophyllus* Greene, Leafl. **2**: 218. 1912.

Stem commonly glabrous except directly under the heads; uppermost leaves ovate, rarely strongly ciliate all around, not at all hairy on the surfaces; phyllaries without hairs. Range of the species, but most common from Idaho and Montana southward.

E speciosus and *E. macranthus* have long been accepted as distinct species, the former supposedly found in the Pacific Northwest, the latter in the Rocky Mountains. Rydberg, and later Blake, recorded *E. speciosus* from the Rocky Mountains, and shortly thereafter Blake named specimens from Washington *E. macranthus*. Examination of the two forms indicates that there is some degree of range correlation, but that either may be expected occasionally in any part of the range. The distinction between the two forms is indeed so tenuous that a good case could be made out for complete reduction of *E. macranthus* to synonomy. Its status as a variety is very weak.

3. ERIGERON PLATYPHYLLUS Greene, Leafl. **1**: 145. 1905. *E. foliosissimus* Greene, Leafl. **2**: 194. 1912. *E. patens* Greene, Leafl. **2**: 194. 1912. *E. rudis* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 184. 1913. *E. semirasus* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 185. 1913.

Perennial herbs with branched woody caudices; stems coarse and stout. 3–8 dm. high or more, only rarely less than 5 dm. high, pubescent at least above with long stiffly spreading hairs, often glandular as well; leaves crowded, more or less triple-nerved, entire but with strongly ciliate margins, at least the middle and upper ones rather densely glandular or more commonly glandular-scabrous, rarely with a few long hairs along the midribs, the basal and lowermost cauline ones oblanceolate to spatulate, narrowed to winged petioles, the blade and petiole mostly 4–15 cm. long and 7–25 mm. wide, often deciduous or withered by flowering time; middle cauline leaves as large as those below, lanceolate to oblong or ovate, sessile, 4–11 cm. long and 10–25 mm. wide, upper leaves not markedly reduced, narrowly lanceolate to narrowly ovate; heads 1–22 in a usually short and broad leafy cyme or cymose panicle, the disks 10–15 (rarely 18) mm. wide and 5–9 mm. high; phyllaries in about two equal series, glandular and sometimes with a few long hairs, the outer ones mostly 0.5–0.9 mm. wide, noticeably broadest near the bases, acuminate, the tips a little loose; ligules numerous, mostly 75–150, about 1 mm. wide and 9–17 mm. long, blue or rarely rose; pappus double. Mountains and woodlands; New Mexico and Arizona.

This species has long passed as a form of *E. macranthus*. The glandular-scabrous leaves and conspicuous spreading hairs on the stem adequately set

it off from that form, although intermediates may be found. Dr. S. F. Blake has recently used the name *E. patens* Greene for this species. Unfortunately, *E. platyphyllus* Greene antedates *E. patens*, and hence must be used, although the cited type is not a very representative form of the species.

E. Vreelandii Rydb., the type of which comes from southern Colorado, just outside the known range of *E. platyphyllus*, was published several months before *E. platyphyllus*. An isotype at hand has distinctly glandular middle and upper leaves, as in *E. platyphyllus*, but lacks the characteristic spreading hairs on the stem. Probably it represents an extreme form of *E. speciosus* var. *macranthus*, the uppermost leaves of which are sometimes very finely glandular. Possibly it may be a hybrid, but I have seen no specimens of *E. platyphyllus* from the area in which it was collected.

4. **Erigeron uintahensis** Cronquist, sp. nov.

Perennial herbs with more or less branched woody caudices; stem 2–5 dm. high, glandular at least above, rather sparsely pubescent throughout with spreading several-celled hairs sometimes as much as 2 mm. long; leaves entire, but with ciliate margins at least toward their bases, the basal and lowermost cauline ones villous-hirsute, sometimes also glandular, oblanceolate, tapering gradually to winged petioles or petioliform bases, the blade and petiole mostly 4–10 cm. long and 6–18 mm. wide, often deciduous by flowering time; middle cauline leaves as large as those below, or larger, oblong or lanceolate to ovate or oval, sessile and somewhat clasping, 3–10 cm. long and 8–20 mm. wide, more or less glandular and sparsely long-hairy; upper leaves not markedly reduced, ovate or lanceolate, glandular and commonly with a few villous hairs; heads 1–5, cymose, the disks 6–9 mm. high and 12–18 mm. broad in pressed specimens; phyllaries in about two equal series, densely glandular and bearing a few villous hairs, the outer ones mostly 0.5–0.9 mm. wide, acuminate or attenuate; ligules numerous, about 75–125, about 1 mm. wide, 9–15 mm. long, blue or rose-purple; pappus double. Uintah Mountains and adjacent area, extending down the Wasatch and adjacent chains to Marysvale, occasional in southern Wyoming.

Herba perennis 2–5 dm. alta parce villosa pilis flexis dispansis certe supra glandulosa aequabiliter foliosa foliis integris, capitulis 1–5 discis 6–9 mm. altis 12–18 mm. latis, bracteis 2-seriatis valde glandulosis et parce villosis, ligulis 75–125, 1 mm. latis 9–15 mm. longis caeruleis, pappo duplico, achaeniis 2-nervosis.

TYPE: *Payson 4894.* Mill Creek, foothills of the Uintah Mountains, sandy river bottom, 8200 feet, July 4, 1926, Summit County, Utah; in the Rocky Mountain herbarium. Isotypes in the herbaria of the University of California, the Missouri Botanical Garden, the United States National Herbarium, and Washington State College.

COTYPE: *Goodman & Hitchcock 1548.* Bear River Valley, dry sagebrush flats, 7900 feet, July 9–13, 1930, Summit County, Utah; in the herbaria of the University of California, the University of Minnesota, the Missouri Botanical Garden, and the Academy of Natural Sciences of Philadelphia.

This endemic has until now passed unrecognized, having been identified by various individuals as *E. speciosus*, *E. macranthus*, *E. viscidus*, and *E.*

subtrinervis, often with a question mark. It is apparently not uncommon in the lower part of the Uintah Mountains, from which about a dozen collections are known. Two collections are known from adjacent Wyoming, and a few from the Wasatch Mountains and their southern extensions. In the Uintahs it is surprisingly constant in appearance, but some specimens from the Wasatch are dubious and perhaps intermediate with *E. speciosus* or *E. subtrinervis*. Its closest relative seems to be *E. platyphyllus*, and the trail of atypical specimens down the Wasatch may represent remnants of an earlier link between the two forms.

5. ERIGERON SUBTRINERVIS Rydb. Mem. Torrey Club **5**: 238. 1894.

Perennial herbs with more or less branched woody caudices; stem 1.5–9 dm. high, pubescent throughout with spreading hairs; leaves more or less triple-nerved, entire but with ciliate margins, densely pubescent along the veins or more or less pubescent throughout, the basal and lowermost cauline ones mostly oblanceolate, narrowed to winged petioles, the blade and petiole mostly 4–13 cm. long and 5–23 mm. wide, often deciduous by flowering time; middle cauline leaves as large as those below, narrowly lanceolate or oblong to broadly ovate, sessile, 3–8 cm. long and 6–27 mm. wide; upper leaves not markedly reduced, narrowly lanceolate to ovate, rarely a little glandular; heads 1–21, cymose or cymose-paniculate, the disks 6–9 mm. high and 13–20 mm. broad; phyllaries in about two equal series, glandular and more or less hirsute or villous, the outer ones mostly 0.4–0.7 mm. wide, acuminate or attenuate, the tips loose; ligules numerous, about 100–150, about 1 mm. wide, 7–18 mm. long, blue or rose-purple; pappus double, the outer commonly setulose. Mountains and woodlands; Washington and Idaho, east to western South Dakota and Nebraska, and south to Utah and New Mexico.

1. Pubescence of the stem and leaves commonly rather dense and uniformly distributed, not obviously denser along the veins; longer hairs of the stem mostly about 1 mm. long or less ..... a. subsp. *typicus*
1. Pubescence of the stem and leaves commonly rather sparse and long, on the leaves often confined chiefly to the margins and larger veins; longer hairs on the stem mostly 1½ mm. long or more ..... b. subsp. *conspicuus*

5a. ERIGERON SUBTRINERVIS Rydb. subsp. **typicus** Cronquist, subsp. nov. *E. glabellus* Nutt. var. *mollis* Gray, Proc. Phil. Acad. **1863**: 64. 1864. *E. subtrinervis* Rydb. Mem. Torrey Club **5**: 238, as to type. 1894. *E. incanescens* Rydb. Bull. Torrey Club **28**: 23, 1901. *E. Bakeri* Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 185. 1913.

Pubescence commonly uniformly distributed and rather dense, if sparse, that on the leaves not confined to the margins and larger veins; longer hairs of the stem mostly 1 mm. long or less, or if obviously longer, then the leaves very densely pubescent. Wyoming, Utah, and New Mexico, east to western Nebraska and South Dakota.

5b. ERIGERON SUBTRINERVIS Rydb. subsp. **conspicuus** (Rydb.) Cronquist, comb. nov. *E. conspicuus* Rydb. Mem. N. Y. Bot. Gard. **1**: 400. 1900. *E. villosulus* Greene, Leafl. **2**: 215. 1912.

Pubescence sparse and long, that on the leaves denser on the margins and main veins, and sometimes confined chiefly thereto; longer hairs on the stem mostly 1½ mm. long or more. Washington, Idaho, Montana, and northwestern Wyoming.

Herbarium records, and my own limited field experience with it, indicate that this species frequents somewhat drier habitats than does its close relative, *E. speciosus.*

6. ERIGERON FORMOSISSIMUS Greene, Bull. Torrey Club **25**: 121. 19 Mr 1898.

Perennial herbs with simple or somewhat branched caudices and fibrous root systems; stems 1–4 (rarely 5.5) dm. high, usually curved or decumbent at the base, more or less glandular at least above, with or without eglandular hairs; hirsute, glandular, or glabrous below; basal and lowermost cauline leaves commonly glabrate or with long scattered hairs, sometimes densely pubescent, oblanceolate or spatulate to oval, entire, commonly rounded or obtuse at the tips, sometimes acute, abruptly narrowed to winged petioles or petioliform bases, the blade and petiole if present mostly 2.5–15 cm. long and 4–15 mm. wide; middle stem leaves lanceolate or oblong, sometimes ovate, commonly somewhat smaller than the lower ones, mostly 2–6 cm. long and 4–16 mm. wide, glabrate or somewhat hirsute, the margins ciliate; upper stem leaves reduced, linear or lanceolate to ovate, the uppermost generally less than 15 mm. long, glandular-scabrous or more or less hairy or both; heads 1–6, cymose, the disks 10–20 mm. broad and 5–10 mm. high; phyllaries in two or three series of about equal length, linear, the outer ones mostly 0.7–1.1 mm. wide (in var. *viscidus* sometimes only 0.6 mm. wide), acuminate, glandular or viscid and often hirsute; ligules numerous, approximately 75–150, 8–15 mm. long and about 1 mm. wide, blue, rarely pink or white; pappus double, the outer setulose and sometimes very scanty. Meadows and open ground in the mountains, often at high altitudes. Arizona, New Mexico, Utah, Colorado, Wyoming, and the Black Hills of South Dakota.

6a. **Erigeron formosissimus** Greene var. **typicus** Cronquist, var. nov. *E. formosissimus* Greene, Bull. Torrey Club **25**: 121, as to type. 1898. *E. hirtuosus* Greene, Leafl. **2**: 209. 1912. *E. subasper* Greene, Leafl. **2**: 195. 1912. *E. fruticetorum* Rydb. Fl. Rocky Mts. 906. 1917.

Involucre glandular and more or less densely hirsute, the long hairs sometimes so numerous as to obscure the glands; basal leaves frequently acutish; uppermost leaves long-hairy or nearly glabrous, with strongly hirsute-ciliate margins, commonly not at all glandular; upper part of the stem glandular and with long spreading hairs. Range of the species.

6b. **Erigeron formosissimus** Greene var. **viscidus** (Rydb.) Cronquist, comb. nov. *E. grandiflorus* Nutt. Jour. Phila. Acad. **7**: 31. 1834. Not *E. grandiflorus* Hook. 1834. *E. eximius* Greene, Pittonia **3**: 295. March 29, 1898. See note under *E. superbus*. *E. viscidus* Rydb. Bull. Torrey Club **28**: 24. 1901. *E. Gulielmi* Greene, Leafl. **2**: 195. 1912. *E. iodanthus* Greene, Leafl. **2**: 209. 1912. *E. rubicundus* Greene, Leafl. **2**: 209. 1912. *E. scaberulus* Greene, Leafl. **2**: 212. 1912. *E. Smithii* Rydb. Bull. Torrey Club **32**: 125. 1905.

Involucre densely glandular, sometimes also with a few long hairs; basal leaves rarely if ever acutish; uppermost leaves glandular-scabrous, commonly without long hairs except for the ciliate margins; upper part of the stem glandular, with or without long spreading hairs. Range of the species.

Forms of *E. formosissimus* var. *typicus* are frequently rather tall, with the upper leaves comparatively little reduced, thus seemingly approaching *E. subtrinervis*. These may be distinguished from that species, however, by the comparatively wide phyllaries with mostly appressed tips.

7. ERIGERON GLABELLUS Nutt. Gen. Pl. **2**: 147. 1818.

Biennial or perennial herbs with simple or slightly branched caudices and fibrous root systems; stems erect, 1–5 (rarely 7) dm. high; herbage sparsely to densely hirsute or strigose with appressed or spreading hairs; basal and lowermost cauline leaves oblanceolate, entire or irregularly toothed, acute to obtuse or rarely rounded at the tips, tapering gradually to winged petioles or petioliform bases, the blade and petiole if present mostly 4–15 cm. long and 3–15 mm. wide; middle stem leaves linear or lanceolate, usually conspicuously smaller than the lower ones, often bract-like; heads 1–15, cymose, usually on long nearly naked peduncles, the disk 10–20 mm. broad, 6–13 mm. high; phyllaries in two or three series of about the same length, sometimes somewhat imbricated, linear, the outer ones mostly 0.5–0.9 mm. wide, acuminate, hirsute or strigose, not glandular, appressed; ligules numerous, about 125–175, 8–15 mm. long, about 1 mm. wide, blue or pink, less commonly white; pappus double, the outer setulose and sometimes very scanty. Meadows, prairies, and open ground; Alaska and Northwest Territory, south to Montana, Utah, South Dakota, and Wisconsin.

1. Pubescence appressed or closely ascending ..... a. subsp. *typicus*
1. Pubescence spreading ..... b. subsp. *pubescens*

7a. **Erigeron glabellus** Nutt. subsp. **typicus** Cronquist, subsp. nov. *E. asper* Nutt. Gen. Pl. **2**: 147. 1818. *E. glabellus* Nutt. Gen. Pl. **2**: 147. 1818. *E. oblanceolatus* Rydb. Bull. Torrey Club **24**: 294. 1897. *E. anicularum* Greene, Leafl. **2**: 215. 1912. *E. anicularum* Greene var. *latiusculus* Greene, Leafl. **2**: 216. 1912. *E. multicolor* Lunell, Am. Midl. Nat. **2**: 255. 1912. *E. obscurus* Lunell, Am. Midl. Nat. **2**: 256. 1912. *E. asper* Nutt. var. *appressus* Lunell, Am. Midl. Nat. **3**: 3. 1913. *E. oligodontus* Lunell var. *acuminatus* Lunell, Am. Midl. Nat. **3**: 4. 1913. *E. subcostatus* Lunell, Am. Midl. Nat. **3**: 5. 1913. *Tessenia glabella Lunell*, Am. Midl. Nat. **5**: 59. 1917.

Most of the names in the above list were transferred to *Tessenia* by Lunell in 1917.

Pubescence appressed or closely ascending, mostly short and fine; crosswalls of the hairs not at all conspicuous if present. Colorado, South Dakota, and Utah, north to southern Manitoba and Saskatchewan.

7b. **Erigeron glabellus** Nutt. subsp. **pubescens** (Hook.) Cronquist, comb. nov. *E. glabellus* Nutt. β *pubescens* Hook. Fl. Bor. Am. **2**: 19. 1834.

E. consobrinus Greene, Pittonia **3**: 186. 1897. *E. fraternus* Greene, Pittonia **3**: 162. 1897. Not *E. fraternus* Greene, Pittonia **2**: 169. 1891. *E. Drummondii* Greene, Pittonia **3**: 295. 1898. *E. Earlei* Rydb. Bull. Torrey Club **32**: 126. 1909. *E. abruptorum* Lunell, Am. Midl. Nat. **3**: 13. 1913. *E. anodontus* Lunell, Am. Midl. Nat. **3**: 6. 1913. *E. asper* Nutt. var. *subinteger* Lunell, Am. Midl. Nat. **3**: 143. 1913. *E. oligodontus* Lunell, Am. Midl. Nat. **3**: 4. 1913. *E. oxyodontus* Lunell, Am. Midl. Nat. **3**: 3. 1913. *E. procerus* Lunell, Am. Midl. Nat. **3**: 5. 1913. *Tessenia glabella* Lunell var. *subdiscoidea* Lunell, Am. Midl. Nat. **5**: 59. 1917.

Most of the names in the above list were transferred to *Tessenia* by Lunell in 1917.

Pubescence spreading, particularly on the stem, often long and coarse; cross-walls of the hairs often highly conspicuous. Alaska and Northwest Territory south to Montana, North Dakota, and Wisconsin; also in Colorado.

E. glabellus subsp. *pubescens* occurs quite commonly in the mountains of Colorado in the same general area that is occupied by subsp. *typicus*. The hypothesis is advanced that subsp. *pubescens*, the ancestral form of the species, migrated north across the plains after the retreating glaciers, giving rise to subsp. *typicus* somewhere in the early part of the migration. Some plants of subsp. *pubescens* remained in the central Rocky Mountains and moved upward in altitude as the climate warmed. These now persist as an island surrounded by plants of subsp. *typicus*.

Dr. Joel Lunell segregated a large number of "new species" from *E. glabellus*. Frequently both subspecies are represented in his type collections, as he worked in an area where the two merge. The reductions made here are based on his type sheets in the University of Minnesota herbarium.

UNIVERSITY OF MINNESOTA
MINNEAPOLIS, MINNESOTA

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 275–288 MAY, 1943

A TAXONOMIC REVISION OF THE GENUS HOLODISCUS (ROSACEAE)

ARLINE LEY

INTRODUCTION

The revision of the genus *Holodiscus* was suggested to me as a taxonomic problem by Dr. Philip A. Munz of Pomona College, to whom I wish to express the deepest gratitude for invaluable guidance and aid. I am also indebted to Mr. G. L. Wittrock of the New York Botanical Garden and to Miss Ruth Sanderson of the Gray Herbarium who have sent me important original descriptions of many species. I should like to thank those in charge of the following herbaria who have kindly loaned their material for this study:

California Academy of Sciences (CAS),
University of Michigan (MICH),
New York Botanical Garden (NY),
Pomona College (POM),
Santa Ana Botanical Garden (RSA),
University of California at Los Angeles (LA),
United States National Herbarium (US)—Mexican and South American specimens.

Abbreviations following the above names are those used in this paper in citation of specimens.

HISTORY OF THE GENUS

The plants now referred to the genus *Holodiscus* were originally included in the genus *Spiraea*. The type species of the genus, collected in New Granada (now Colombia) by Mutis, was described as *Spiraea argentea* by Linnaeus f., Suppl., 261 (1781). In 1836 Rafinesque applied the name *Schizonotus* to the species *Spiraea discolor* Pursh (Fl. Am. **1**: 342. 1814). In New Fl. **3**: 74 (1836) he stated that he "adopted the Genus and name *Schizonotus* upon the suggestion of Lindley," but he did not know how the name "split back" applied "unless the capsules open outside." In Sylva Tell., 152 (1838) he applied the name *Sericotheca* (from the Latin, "silky" and "case," referring to the hairy carpels) based on the species *Spiraea argentea*. The name *Schizonotus* Lindl. had already been established as a synonym for *Spiraea Lindleyana* Wall. by Lindley (ex Wall. Cat. n. 703. 1830), but had become obsolete. Rafinesque took the name and applied it here.

The name *Holodiscus* (from the Greek, "whole" and "disk," referring to the entire disk of the flower) was first applied to this group by Koch,

Dendr. **1**: 309 (1869), who made it a section under *Spiraea*, based on *Spiraea ariaefolia* Smith (in Rees, Cycl. **33**: no. 16. 1819). Maximowicz, Acta Hort. Petrop. **6**: 253 (1879), used the name *Holodiscus* in the tribe Potentilleae. It was later placed in a special tribe, Holodisceae, by Focke in Engler and Prantl, Nat. Pfl. **3** (3) : 18 (1894). Focke separated the genus from *Spiraea* because of the one-seeded indehiscent fruit. He recognized two species, *H. discolor* (Pursh) Maxim. and *H. argenteus* (L.f.) Maxim.

In 1891 O. Kuntze, Rev. Gen. **1**: 225, again used the name *Schizonotus* for the genus and recognized only one species, *Schizonotus argenteus* (L.f.) Kuntze, with ten varieties. Schneider, Handb. Laubh. **1**: 495 (1905), in his treatment of the genus placed it under the subfamily Holodisceae, calling the genus *Holodiscus*. He was not satisfied with Kuntze's treatment of the group and recognized five species which he divided into two main types: those of the United States, and those of Mexico and South America. His five species included: *H. discolor, H. dumosus, H. australis, H. fissus,* and *H. argenteus.*

The genus was last revised as a whole by Rydberg (N. Am. Fl. **22**: 261. 1908) who revived the name *Sericotheca* and placed the genus under the tribe Holodisceae. He recognized fourteen species: 9 United States and 5 Mexican and South American species. *Schizonotus* Raf. has now been rejected, and *Holodiscus* Maxim. is placed in the Nomina Conservanda of the International Rules of Botanical Nomenclature, 98 (1935).

CHARACTERS USED IN CLASSIFICATION

The species of the genus *Holodiscus* are found to intergrade to some extent in most cases. The most consistent character used in classification is the leaves. The size, shape, pubescence, and glandular condition of the leaves, as well as the nature of the petiole and teeth, are the important key characters in the genus. While these intergrade to varying degrees, the groups can usually be readily separated on this basis. The length and shape of the sepals are not consistent throughout, although Rydberg used these to separate certain species. In the same way the nature of the inflorescence is not consistent enough to be used in distinguishing species. The pubescence on the backs of the petals proves to be denser in some species and is a fairly reliable character in separating the United States forms from those to the south.

In general, two principal groups might be separated: one ranging from British Columbia through western United States to northern Mexico; and another, from central Mexico south to Colombia. The southern group is distinct in having long, pointed mucros on the teeth which are often bent, in the greater length of the leaf-blades as compared to the width, and in the greater pubescence on the outer surface of the petals.

DESCRIPTION OF THE GENUS

Holodiscus Maxim. Acta Hort. Petrop. **6**: 253. 1879; Kuntze, Rev. Gen. **1**: 225. 1891; Engler & Prantl, Nat. Pfl. **3**(3): 18. 1894; Schneider, Handb. Laubholzk. **1**: 495. 1905.

Spiraea § *Holodiscus* K. Koch, Dendr. 1: 309. 1869.

Spiraea § *Spiraria*, Sér. in DC. Prod. 2: 544, in part. 1825.

Spiraea Endlicher, Gen. Pl. 1247, in part. 1840; Benth. & Hooker, Gen. Pl. 1(2): 611. 1865; Brewer & Wats. Bot. Calif. 1: 170. 1876.

Schizonotus Raf. New Fl. 3: 74. 1836. Not *Schizonotus* Lindl. 1830; Piper, Contr. U. S. Nat. Herb. 11: 330. 1906.

Sericotheca Raf. Sylva Tell. 152. 1838; Rydb. N. Am. Fl. 22: 261. 1908.

Sepals 5, 3-nerved, valvate in the bud, erect in fruit. Petals 5, short-clawed or rounded. Hypanthium saucer-shaped, adnate to base of calyx; disk entire. Stamens usually 20, inserted on disk with 3 stamens opposite each petal, one opposite each sepal; anthers didymous. Pistils 5, distinct, alternate with sepals, villous, inserted on center of disk, sessile; styles terminal; ovules 2, collateral, pendulous. Fruit indehiscent, one-seeded, enclosed in the calyx, short-stipitate, laterally flattened, villous, membranaceous, caducous, convex on lower suture. Seeds pendulous, broadly oblong, with double coat, thin endosperm; embryo with superior radicle and ovate cotyledons. Shrubs or small trees, spreading, to 7 m. tall, with alternate, simple, toothed leaves; stipules lacking. Inflorescence terminal with whitish or pinkish flowers, villous, racemose or paniculate.

TYPE SPECIES: *H. argenteus* (L.f.) Maxim. The genus is distributed from Canada south throughout western United States to South America.

KEY TO SPECIES

A. Teeth ending in a short, straight, rounded mucro; petals with a few long hairs at outer base; stamens longer than sepals.

B. Leaf-blades toothed along sides below middle, elliptic to orbicular, not obovate.

C. Leaves elliptic to elliptic-ovate or ovate, longer than broad, with 3–6 teeth on each side, usually deeply toothed, glabrous or with a scattered pubescence above.

D. Leaves not decurrent on petiole but contracted at base forming a distinct petiole, teeth usually divided 3–6 times except in var. *delnortensis*. Coastal British Columbia to Southern Calif. 1. *H. discolor.*

DD. Leaves decurrent on petiole, teeth usually simple, rarely doubly divided.

E. Leaves deeply toothed, teeth narrow, leaf blades narrowly cuneate at base. Wyoming to Arizona and Chihuahua 2. *H. dumosus.*

EE. Leaves not deeply toothed, teeth broad and rounded, leaf blades very broad at base, abruptly contracted. Valley of Mexico 3. *H. pachydiscus.*

CC. Leaves broadly ovate to orbicular, almost as broad as long, with 3–4 teeth on each side, not deeply toothed, pubescent to villous above, blades abruptly contracted, forming a short winged petiole. Mts. of California 4. *H. Boursieri.*

BB. Leaf-blades toothed at top, rarely to middle, obovate to spatulate. Mts. from Oregon to Baja California 5. *H. microphyllus.*

AA. Teeth ending in a long, pointed, often bent mucro; petals with a scattered, often dense pubescence on outer side; stamens not longer than sepals.

B. Leaf-blades acute at apex, linear to lanceolate, tomentose to villous beneath.

C. Leaf-blades 4–5 times as long as wide, almost entire, the teeth scarcely noticeable. Orizaba . . 6. *H. orizabae.*

CC. Leaf-blades 2–3 times as long as wide, coarsely toothed. Michoacán and Guerrero (Mexico) to Guatemala . 7. *H. fissus.*

BB. Leaf-blades obtuse to rounded at apex, oblanceolate to obovate, white silky beneath. Oaxaca (Mexico) to Colombia . 8. *H. argenteus.*

TREATMENT OF SPECIES

1. HOLODISCUS DISCOLOR (Pursh) Maxim. Acta Hort. Petrop. **6**: 254. 1879.

A tall spreading shrub, 1.5–6 m. tall; bark of older branches dark-reddish to chestnut brown, becoming dark gray and exfoliating; young twigs light, straw-colored, pubescent, even villous; internodes about one-half the length of leaves; leaf-blades ovate to ovate-elliptic or -oblong, either truncate or cuneate at base, not decurrent on the distinct petiole, the apex rounded to obtuse, teeth deep, broad and round, ending in a short mucro, usually with 4–6 teeth on each side, each tooth divided 1–6 times except in var. *delnortensis*, the leaves gray-green to green above, sparingly pubescent, usually paler beneath, pubescent to villous or tomentose, the leaf-blades 3.0–8.0 cm. long and 2–7 cm. wide; petioles 0.5–2.5 cm. long; inflorescence spreading, dense, very compound, villous, 5–25 cm. long, and 5–25 cm. wide; pedicels 1.5–3.0 cm. long, with linear bracts 1 mm. long; sepals triangular-ovate to elliptic-ovate, acute to obtuse at apex, 1.5–2.0 mm. long; petals oval, 2 mm. long, with several hairs on the outer base; stamens longer than sepals; carpels very villous, up to 1.5 mm. long; styles up to 1 mm. long; achenes with straight upper edge and very much convex lower edge.

KEY TO VARIETIES

Leaf-blades at least 4.5 cm. long, 3–7 toothed on either edge, and with short pubescence on lower surface. British Columbia to Montana and Southern California 1a. *H. discolor* var. *typicus.*

Leaf-blades less than 4.5 cm. long, 2–4 toothed on either edge, often with many long hairs beneath.

Teeth of leaves compound, leaves grayish beneath, petioles 5–8 mm. long. Southern Oregon to Southern California 1b. *H. discolor* var. *franciscanus.*

Teeth of leaves usually simple, leaves whitish beneath, petioles 6–12 mm. long. Crater Lake, Oregon, to Del Norte Co., California. 1c. *H. discolor* var. *delnortensis.*

1a. H. DISCOLOR var. **typicus** Ley, var. nov.

Spiraea discolor Pursh, Fl. Am. 342. 1814; *Schizonotus discolor* Raf. New Fl. 3: 75. 1836; *Holodiscus discolor* Maxim. Acta Hort. Petrop. **6**: 254. 1879; *Schizonotus argenteus* var. *discolor* Kuntze, Rev. Gen. 1: 225. 1891; *Sericotheca discolor Rydb.* N. Am. Fl. **22**: 262. 1908; *Spiraea ariaefolia* Smith, in Rees' Cycl. **33**: no. 16. 1819; *Spiraea discolor* var. *ariaefolia* S. Wats. Bot. Calif. 1: 170. 1876; *Schizonotus argenteus* var. *ariaefolius* Kuntze, Rev. Gen. 1: 225. 1891; *Schizonotus ariaefolius* Greene, Fl. Fran. 58, in part. 1891; *Schizonotus discolor* var. *Purshianus* Rehder in Bailey, Cycl. Am. Hort. **4**: 1627. 1902.

Illustration: Figure 8.

Leaf-blades broadly ovate with a truncate base, to ovate-elliptic with cuneate base, villous-pubescent to tomentose beneath, 4.5–7 (10) cm. long, 2.5–8 cm. wide, the petioles 0.7–2 cm. long; inflorescence spreading, 7–20 cm. long, 5–20 cm. wide.

There has been a great deal of confusion concerning the species *Spiraea ariaefolia* Sm., *S. discolor* Pursh and *S. dumosa* Nutt. By some *S. ariaefolia* is treated as the coastal form, and *S. discolor* Pursh and *S. dumosa* Nutt, as the Rocky Mountain form. Other investigators feel that *S. ariaefolia* Sm. and *S. discolor* Pursh are in the same species, and the *S. dumosa* Nutt. is different. From the literature and specimens reviewed, it would seem that the Rocky Mountain material is very different from the specimens of the northwest. I have not seen type material of *S. dumosa* Nutt., but from descriptions of Torrey (Ann. Lyc. N. Y. **2**: 195. 1827), Torrey and Gray (Fl. N. Am. **1**: 416. 1840), and Hooker (Lond. Jour. Bot. **6**: 217. 1847), I believe it to be entirely different from *S. ariaefolia* Sm. and *S. discolor* Pursh. These two are here considered the same form and are included under *H. discolor* var. *typicus*.

This variety cannot be clearly distinguished in all cases from var. *franciscanus*. The two intergrade in the size and thickness of the leaves in the counties about San Francisco Bay, as for example do the following specimens from that region: Leona, Alameda Co., *Michener and Bioletti in 1892* (NY); Oakland Hills, near San Francisco, Alameda Co., *Torrey 133* (NY); and Los Troncos Creek, San Mateo Co., *Berry in 1909* (POM). These specimens resemble var. *franciscanus* in leaf form, but are 4.5 cm. long. There are a few forms which might be included with var. *franciscanus* because of their small leaf size, such as the specimens: MONTANA: Bigfork, Flathead Lake, Flathead Co., *Jones 8300* (POM); and Flathead Valley, *MacDougal 757* (NY). B.C.: Goldstream, Vancouver Is., *Macoun in 1887* (NY). WASHINGTON: Friday Harbor, San Juan Co., *Heller 970* (LA, NY); Tacoma, Pierce Co., *Millis in 1883* (NY). OREGON: unknown locality, *Spalding* (NY), Mt. Hood, *Jones in 1897* (POM); the Dalles, Wasco Co., *Jones in 1897* (POM). However, I feel that these are exceptions and should be included under var. *typicus* because of the very broad inflorescence and the thin leaves in most cases, as well as because of their distribution.

TYPE collected by Lewis on the banks of the Kooskoosky, Idaho. Range, along streams, on rocky hillsides or in open woods, between 50 and 4500 feet, from B. C. to Mont. and Coastal S. Calif. *Representative material:* MONTANA: Hitchcock 1671, 1886. IDAHO: *MacDougal 176, Leiberg 1310, Aiton 6171, Sandberg 583, M. E. Jones 6285, Clark 171.* B. C.: *Eastwood 9909, Macoun 34817, 34818.* WASHINGTON: *Elmer 2522, Heller 4025, Allen 2, Thompson 9818.* OREGON: *Menzies*, part of type collection of *ariaefolia* (NY), *Sheldon 10977, Jones 4210.* CALIFORNIA: *Heller 7511, Hoffman 645, no. 9, Eastwood 6164, Munz 2218, Abrams 1723.*

1b. H. DISCOLOR var. FRANCISCANUS (Rydb.) Jepson, Fl. Calif. **2**: 166. 1936.

Sericotheca franciscana Rydb., N. Am. Fl. 22: 262. 1908; *Holodiscus franciscanus* Rehder, Jour. Arnold Arb. 1: 260. 1920.

Illustration: Figure 9.

Leaf-blades thick, usually broadly ovate with truncate base and rounded

apex, villous beneath, usually 3–4.25 cm. long, 2–3 cm. wide, petioles 0.5–0.8 cm. long; inflorescence 7–12 (18) cm. long, 6–12 cm. wide.

TYPE: San Leandro, Alameda Co., Calif., *L. M. Underwood in 1888* (NY). Range, on open hillsides or along streams, between 300 and 2900 ft., S. Ore. to Orange Co., Calif. *Representative material:* OREGON: *Heller 13070, 12634.* CALIFORNIA: *Butler 1645, Heller 11545, 12362, 5729, Abrams 5920, Jones 3579, Keck 1795, Elmer 4274, Stark 2248.*

As has been noted above under the variety *typicus*, there are a few plants found about San Francisco Bay which intergrade with that variety in leaf-size, for example: *Eastwood 4733, Michener & Bioletti* in 1892, *Carruth* in 1901. Because of their thick leaves they are placed under var. *franciscanus*, although rather large.

1c. H. DISCOLOR var. **delnortensis** Ley, var. nov.

Folia ovata cum basi cuneato, supra grisea et pubescentia, infra tomentosa et alba, simplice dentata; laminis foliorum 1.5–3.5 cm. longis, 1–2 cm. latis; petiolis 0.6–1.2 cm. longis; inflorescentia 6–14 cm. longa, 3–7 cm. lata.

Illustration: Figure 10.

TYPE: Darlingtonia, Smith River, Del Norte Co., Calif., *H. E. & S. T. Parks 24019*, POM. no. 257430; isotypes RAS, NY, CAS. Range from Crater Lake, Oregon to Del Norte Co., California; represented by: OREGON: *Jones 7723, 7752.* CALIFORNIA: *Abrams 8436, Wolf 864, 9127, Eastwood 12195, 2131.*

This variety is very close to *H. discolor* var. *franciscanus*, but differs in the very white appearance of the undersides of the leaves and in having simple teeth. There is a tendency for this group to have a longer petiole as compared to the length of the leaf blade than in the other two varieties. The shape of the leaf is very characteristic, the leaf-blade being narrow at the top, broad near the base, and becoming cuneate.

2. HOLODISCUS DUMOSUS (Nutt.) Heller, Cat. N. Am. Pl. 4. 1898.

A spreading shrub, 1–3 m. tall; bark of older twigs dark red, later becoming dark gray and exfoliating; young twigs light, often straw-colored, very villous, the internodes from much less than, up to length of leaves; leaf-blades elliptic or elliptic-ovate with cuneate base decurrent on petiole, the apex rounded to obtuse, the teeth rather deep, usually simple, sometimes double, ending in a short, blunt mucro, mostly with 3–6 teeth on each side, the leaves gray-green above and glabrous, or slightly pubescent between veins, either whitish beneath and both tomentose and villous with long silky hairs especially along veins, or sparingly pubescent beneath with gland droplets between veins, the leaf-blades 1–3.5 (5) cm. long and 0.5–2 cm. wide, the petioles 0.2–1 (1.4) cm. long; inflorescence with spreading branches, compound especially in lower part, densely villous, 5–20 cm. long, 3–10 cm. wide; pedicels 2–3 mm. long, subtended by linear bracts scarcely 1 mm. long; sepals triangular-ovate, 1.5–2 mm. long; petals oval, rarely with several long hairs at base beneath, 2 mm. long; stamens slightly longer than sepals; carpels very villous, 1 mm. long; styles 1 mm. or less, achenes with straight upper edge and very much convex lower edge.

KEY TO VARIETIES

Leaf-blades pubescent to villous, not glandular beneath.

Leaf-blades pubescent beneath, rarely villous, 1–2 cm. long, about twice as long as wide; inflorescence small and spreading. Wyoming to eastern Utah and Colorado . . . 2a. *H. dumosus* var. *typicus.*

Leaf-blades very villous beneath, 2.3–5 cm. long, more than twice as long as wide; inflorescence large and spreading. Southeastern Colorado to Arizona and Chihuahua 2b. *H. dumosus* var. *australis.*

Leaf-blades scarcely pubescent beneath with long hairs along veins and with gland droplets between veins, 1.5–2.5 cm. long, about twice as long as wide. San Luis Potosí, Mexico 2c. *H. dumosus* var. *Schaffneri.*

2a. H. DUMOSUS var. **typicus** Ley, var. nov.

Spiraea dumosa Nutt. ex Torr. & Gray, Fl. N. Am. 1: 416, as syn. 1840; Hooker, London Jour. Bot. 6: 217. 1847; *Spiraea discolor* var. *dumosa* S. Wats. Bot. Calif. 1: 170, in part. 1876; *Schizonotus argenteus* var. *dumosus* Kuntze, Rev. Gen. 1: 226, in part. 1891; *Holodiscus discolor* var. *dumosus* Dippel, Handb. Laubh. 3: 508. 1893; *Schizonotus dumosus* Koehne, Deuts. Dendr. 265. 1893; *Holodiscus dumosus* Heller, Cat. N. Am. Pl. 4. 1898; *Schizonotus discolor* var. *dumosus* Rehder, Cycl. Am. Hort. 4: 1629, in part. 1902; *Sericotheca dumosa* Rydb. N. Am. Fl. 22: 263. 1908.

Illustration: Figure 5.

Frequently a low shrub about 1 meter high; leaf-blades usually less than 2 cm. long and about half as wide, usually slightly villous, teeth most often rounded, not usually pointed; inflorescence branched, 5–12 cm. long, 2–7 cm. wide.

TYPE collected by Nuttall, stony and sandy places of the Platte River. Growing among rocks or brush, between 2300 and 9400 ft., Wyo. and Colo. to eastern Utah and northern Arizona. *Representative material:* WYOMING: *Nelson 657, 9247, 7481.* UTAH: *Goodding 1271, Rydberg & Garrett 9468.* COLORADO: *Palmer 38122, Osterhout 2121, Patterson 22, Baker 264.* ARIZONA: *Toumey* in 1892, *Osterhout 6986, Eastwood 5889, Rusby 588.*

2b. H. DUMOSUS var. **australis** (Heller) Ley, comb. nov.

Holodiscus australis Heller, Bull. Torrey Club 25: 194, *pl. 338.* 1898.

Illustration: Figure 4.

Shrub 2–3 m. high; leaf-blades usually densely villous and tomentose beneath, 2–3 (5) cm. long, less than half as wide, the teeth usually drawn out and pointed; inflorescence spreading, 6–20 cm. long, 3–6 cm. wide.

Type collection, from Santa Fé Cañon, 9 mi. east of Santa Fé, New Mexico, *Heller 3840.* Growing in dry rocky places between 7000 and 11000 ft., southeastern Colorado to Arizona, Texas, and Chihuahua. *Representative collections:* COLORADO: *Clements 127, Clokey 3791, Rollins 1841.* ARIZONA: *Jones 3960, Wolf 3151, Peebles & Harrison 2255, Blumer 1281.* NEW MEXICO: *Wolf 2714, 2812, Metcalfe 250, 1171, Wooton 284.* TEXAS: *Moore & Steyermark 3572, Ferris & Duncan 2530.* CHIHUAHUA: *Pringle 7831, Goldman 1414, Nelson 4874.*

The following specimens have small leaf-blades, but the slender narrow leaf and pointed teeth would indicate that they belong in this group: ARIZONA: *Griffiths & Thornber 165.* NEW MEXICO: *Diehl 452.* TEXAS: *Mueller 8288.* CHIHUAHUA: *Barber & Townsend 144, 147, Nelson 6150, Mueller 1242.*

Rydberg (N. Am. Fl. **22**: 263. 1908) does not separate *australis* from the more northern material and merely recognizes it as "the form with thinner, more acutish leaf-blades and more simple toothing." As a whole it differs in leaf-size, breadth-to-length ratio, toothing and length of sepals.

2c. H. DUMOSUS var. **Schaffneri** (Rydb.) Ley, comb. nov.

Sericotheca Schaffneri Rydb., N. Am. Fl. 22: 264. 1908; *Holodiscus Schaffneri* Standley, Pub. Field Mus. Bot. 4: 210. 1929.

Leaf-blades scarcely pubescent beneath with long hairs on veins and with gland-droplets between veins, the teeth broad and rather rounded; leaf-

blades 1.5–4.5 cm. long, about half as wide; inflorescence 4–8 cm. long, 3–7 cm. wide.

TYPE: San Luis Potosí, Mexico, *Schaffner 457*. Known only from the type region, from such collections as *Parry & Palmer 223, Mueller 2222, Lundell 5391.*

3. HOLODISCUS PACHYDISCUS (Rydb.) Standley, Pub. Field Mus. Bot. **4**: 210. 1929.

Sericotheca pachydisca Rydb., N. Am. Fl. 22: 263. 1908.

Illustration: Figure 7.

Older branches dark-gray with exfoliating bark, angled; young twigs light reddish-brown, pubescent, angled, internodes about one-half length of leaves; leaf-blades broadly ovate, more or less abruptly contracted at base with a short winged petiole, the apex obtuse, many-toothed, the teeth very broad and rounded, simple, ending in a short, blunt mucro, 3–4 on each side, the leaves pubescent above, grayish and villous beneath, the blades 1.5–3 cm. long, 0.8–2.5 cm. wide; petioles 2–3 mm. long; inflorescence spreading, compound, with a short dense pubescence, 3.5–15 cm. long, 3–15 cm. wide; pedicels 2–3 mm. long, with three linear bracts up to 2 mm. long; sepals triangular-ovate, glabrous within, acute at apex, 1.5 mm. long; petals elliptical, 1.5–2 mm. long; stamens as long as sepals, inserted on a thick fleshy hypanthium; carpels very villous.

TYPE: Valle de Mexico, Tacuboya, *Bourgeau 267* (US. Photo of type, NY). Known only from a single collection.

4. HOLODISCUS BOURSIERI (Carr.) Rehder in Bailey, Cycl. Hort. 1498. 1915.

Spiraea Boursieri Carr. Rév. Hort. **1859**: 520, *f. 108*. 1859; *Sericotheca Boursieri* Rydb. N. Am. Fl. 22: 263. 1908; *Holodiscus saxicola* Heller, Muhlenbergia 1: 41, 1904; *Sericotheca saxicola* Rydb. N. Am. Fl. 22: 263. 1908; *Sericotheca obovata* Rydb. N. Am. Fl. 22: 264. 1908.

Illustration: Figure 6.

A low shrub up to 1 m. high; bark of older branches dark reddish, becoming dark gray, exfoliating; young twigs straw-colored, often angled, short-pubescent to villous-pubescent, internodes from half as long as to as long as leaves; leaf-blades broadly obovate to orbicular, the base sometimes cuneate, more or less abruptly contracted, forming a short, winged petiole, the apex broad and rounded, many-toothed, the teeth broad and rounded, not deep, ending in a very short, blunt mucro, usually 3–4 teeth on each side extending at least to middle of leaf-blade, the leaves green or gray-green above, finely to villous-pubescent, grayish or whitish beneath, villous to villous-tomentose, often glandular, the leaf-blades 1–3 cm. long, 1–2.5 cm. wide; petioles 2–3 mm. long; inflorescence narrow to spreading, villous, 2.5–8 cm. long, 2.5–8 cm. wide; pedicels 1–2 mm. long, with three bracts, linear to narrowly lanceolate, 1 mm. long; sepals triangular-ovate with acute apex, 1.5–2 mm. long; petals oval, 2 mm. long, with a few long hairs at outer base; stamens longer than sepals; carpels villous, 1.5 mm. long, styles 1 mm. long, achenes with straight upper edge and very convex lower edge.

Type locality, California. Growing among rocks, between 4600 and 8000 feet, in the mountains of California and adjacent Nevada. *Representative specimens:* CALIFORNIA: *Train 250, Howell 13493, Hitchcock & Martin 5357, Jones 2506, Heller 14451, 7160* (type no. of *H. saxicola*), *12896, Crum 2078, Johnston 1566, Everett 7221, Wolf 5390.* NEVADA: *Greene 1431.* Intermediate between *H. saxicola* and *Boursieri*, as separated by

some authors, are *Hansen 234, Bracelin 913, Eastwood 249*; for this reason I cannot maintain two separate entities. Although I have not seen the type of *Spiraea Boursieri* Carr., the figure given in the original description is well matched by *Heller 12896, Everett 7221, Johnston 1566.*

5. HOLODISCUS MICROPHYLLUS Rydberg, Bull. Torrey Club **31**: 559. 1904.

Low spreading shrub, 15 cm. to 2 m. high; bark of older twigs dark red, later becoming dark gray and exfoliating; young twigs reddish tan to light tan, glabrescent with gland droplets to villous-pubescent, the internodes from one-half as long as to as long as leaves; leaves in fascicles of 1–8, obovate to spatulate with cuneate base decurrent on petiole, the apex rounded, many-toothed, the teeth usually small, broad, and rounded, often ending in a short, blunt mucro, 2–3 on each side, the leaf-blades toothed only above middle, light green or gray green above, glabrescent to villous above, glabrescent with gland droplets to villous-tomentose beneath, white-silky beneath in some, the leaf-blades 0.5–1.75 cm. long, rarely 2 cm. long, 0.3–1 cm. wide; petioles 1–2 mm. long; inflorescence usually narrow and compact, rarely compound, villous, 2.5–3.5 cm. long, 1–3 cm. wide; pedicels 1–3 mm. long with linear bracts, 1 (rarely 2) mm. long; sepals narrow, triangular-elliptic with acute apex, 1–1.5 mm. long; petals oval to elliptic, 1.5–2 mm. long, glabrous beneath or with a few long hairs at outer base; stamens longer than sepals; carpels villous, 1 mm. long, styles 1 mm. long, achenes with straight upper edge and convex lower edge.

KEY TO VARIETIES

Leaf blades pubescent to villous beneath, with hairs masking gland-droplets if these are present, often pubescent above.

Leaf-blades villous beneath, finely to densely pubescent above. Idaho, to California, and Colorado 5a. *H. microphyllus* var. *typicus.*

Leaf-blades densely white-silky beneath, villous above. Clark Co., Nevada, Arizona, and San Jacinto Mts., California, Lower California. 5b. *H. microphyllus* var. *sericeus.*

Leaf-blades glabrescent to glabrous beneath with evident gland-droplets between veins, glabrescent or with a scattered pubescence above. Mts. from Oregon and California to Utah 5c. *H. microphyllus* var. *glabrescens.*

5a. H. MICROPHYLLUS var. **typicus** Ley, var. nov.

Holodiscus microphyllus Rydb. Bull. Torrey Club **31**: 559. 1904; *Sericotheca microphylla* Rydb. N. Am. Fl. **22**: 264. 1908; *Holodiscus discolor* var. *microphyllus* Jepson Fl. of Calif. **2**: 166. 1936; *Sericotheca concolor* Rydb. N. Am. Fl. **22**: 264. 1908.

Illustration: Figure 1.

Leaf-blades pubescent to villous above, villous beneath, 0.5–2 cm. long, 0.3–1.2 cm. wide; inflorescence 3.5–9 cm. long, 1.5–7 cm. wide.

TYPE from Alta, Wasatch Mts., Utah, based on *Jones 1142* (NY, POM); range from California to Idaho and western Colorado. *Representative collections*: CALIFORNIA: *Heller 12135, Bracelin 888, Grant 1134, Eastwood 1332, Crafts 625, Munz 14819, 7625, Wolf 1699, 7644, 7649, Johnston 1696.* NEVADA: *Heller 10353, 9542, Duran 3104.* UTAH: *Eastwood 7705, Jones 5531.* COLORADO: *Baker, Earle & Tracy 8631.* ARIZONA: *Jones 6056.*

5b. H. MICROPHYLLUS var. **sericeus** Ley, var. nov.

Laminae foliorum supra villosae, infra albido-sericeae, 0.5–2 cm. longae, 0.4–1 cm. latae; inflorescentia 3–6 cm. longa, 1–4 cm. lata.

TYPE: Griffiths Mine, bottom of rocky ravine, Clark Co., Nevada, *Clokey 7969* (POM 257589; isotypes NY, RAS). Ranging from southern Nevada to Lower California. Material seen: NEVADA: Potosi Mt., *Jaeger* in 1930 (POM); *Heller 11006, Clokey 7556, 7138, 5507*. ARIZONA: Huachuca Mts., *Hilend* in 1931 (LA). CALIFORNIA: San Jacinto Mts., *Jaeger* in 1921 (POM). LOWER CALIFORNIA: *Wiggins & Demaree 5037, Goldman 1222.*

This variety might be confused with forms of *typicus* having densely villous leaves, but is more silvery beneath and with a greater contrast between pubescence on the upper and lower surfaces than in *typicus*, which is almost equally villous on both surfaces.

5c. H. MICROPHYLLUS var. **glabrescens** (Greenman) Ley, comb. nov.

Spiraea discolor var. *glabrescens* Greenman, Erythea 7: 116. 1899; *Holodiscus glabrescens* Heller, Muhlenbergia 1: 40. 1904; *Sericotheca glabrescens* Rydb. N. Am. Fl. **22**: 264. 1908; *H. discolor* var. *glabrescens* Jepson, Man. Fl. Pls. Calif. 479. 1925.

Leaf-blades glabrescent to glabrous above, glabrescent to glabrous beneath with many gland droplets between veins, 0.5–2 cm. long, 0.2–1.5 cm. wide; inflorescence 3–10 cm. long, 1–7 cm. wide.

TYPE from Stein's Mt., Oregon, *Cusick 1253* (NY); ranging through mountains of Oregon and California to Utah. *Representative numbers:* OREGON: *Cusick 2716, 1968, Hitchcock 4908, Abrams 9600, Thompson 12195*. CALIFORNIA: *Copeland, 375, 3781, Heller 11667, 11730, Cooke 11505*. UTAH: *Leonard 129, Eastwood & Howell 7169, Cottam 4535.*

In inflorescence, habit, leaf-size and -shape, this variety resembles var. *typicus;* it differs in the glabrescence of the leaves and the evident gland-droplets beneath.

6. **Holodiscus orizabae** Ley, sp. nov.

Illustration: Figure 2.

Rami subrubentes ad grisei, decorticantes; ramulis angulatis, villosis, internodiis plus quam dimidio longitudinis foliorum; laminis foliorum lanceo-ellipticis, angustissimis, cum base cuneato, in petiolis decurrentibus, apice acuto in mucro longissimo terminando, foliis subintegris, dentibus obscuris, mucronatis, tres utrimque, laminis foliorum in superficie superiore glabris vel pubescentibus, inferiore tomentoso-villosis, 2–3 cm. longis, 0.6–1 cm. latis; inflorescentia ampla, composita, 6–10 cm. longa, 4–8 cm. lata; pedicellis 0.3–0.5 cm. longis cum tres bracteis lanceolatis, 2–3 mm. longis; sepalis late triangulo-ovatis, ad apicem acutis, 2 mm. longis; petalis late ovatis ad orbiculatis, infra pubescentibus, in nervo mediano sericeis, 2 mm. longis, stylis 1 mm. longis, acheniis cum margine superiore leviter curvata et inferiore gibbissima.

TYPE: Vaquería de Jacal, Pico de Orizaba, Mexico, 10–11000 ft. *Liebmann 1670* (US, 1012847; isotypes, NY). Known only from the type collection.

The very narrow leaves of this species set it apart from any other form, and it seems advisable to recognize it as a distinct species. It corresponds in leaf-shape to the description in O. Kuntze's key (Rev. Gen. 1: 226. 1891) of *Schizonotus argenteus* var. *angustissimus*. However, his description is very short and no specimens were cited by him. As I have not seen any specimens of this species annotated by him, I cannot with any degree of certainty designate this as the form to which he refers.

7. HOLODISCUS FISSUS (Lindl.) Schneider, Ill. Handb. Laubh. 1: 495. 1905.

Spiraea fissa, Lindl., Bot. Reg. 2, misc., 73. 1840; 28, Misc., 1. 1842; *Schizonotus argenteus* var. *fissus* Kuntze, Rev. Gen. 1: 226. 1891; *Schizonotus discolor* var. *fissus*

Rehder in Bailey, Cycl. Am. Hort. 1627. 1902; *Sericotheca fissa* Rydb. N. Am. Fl. 22: 265. 1908; *Spiraea argentea* Benth. Pl. Hartw. 82. 1841. Not *S. argentea* L. f. 1781. *Holodiscus argenteus* var. *bifrons* Focke, Bot. Gaz. 18: 200. 1893; *Holodiscus Loesceneri* Dammer, Repert. Sp. Nov. **25**: 385. 1919.

Illustration: Figure 11.

Slender shrub 2–3.5 m. high; branches angled, more deeply ribbed in younger twigs, older branches dark red to dark gray, exfoliating; young twigs tan to light reddish-brown, with a short, dense pubescence, sometimes villous, the internodes ¼ to ½ length of leaf; leaf-blades lanceolate to oval, cuneate at base, decurrent on petiole, acute to acuminate at apex, ending in a sharp mucro, the teeth conspicuous, usually ending in a long, sharp mucro, frequently bent, 5–9 teeth on each side with many small teeth near apex, the leaf-blades glabrous above or rarely with a scattered pubescence in young leaves, with a short, dense pubescence beneath, often villous, particularly along veins, 2.5–8 cm. long, 1–4 cm. wide; petioles 0.5–1.5 cm. long; inflorescence sparse, spreading, villous, 9–20 cm. long, 5–15 cm. wide; pedicels 2–3 mm. long with lanceolate bracts, these 1–3 mm. long, up to 1 mm. wide; sepals triangular with acute apex, 1–2 mm. long; petals oval to orbicular with fine pubescence scattered over back, particularly along veins, 2 mm. long; carpels villous, 1–2 mm. long; styles 1–2 mm. long; achenes with slightly curved upper edge and convex lower edge.

TYPE collected by Hartweg in Mexico. Range, southern Mexico to Guatemala. *Material seen:* MEXICO—MICHOACÁN: *Nelson 6583* (NY, US). GUERRERO: *E. Nelson 2210* (NY, US). OAXACA: *Smith 822* (US), *Camp 2637* (NY). CHIAPAS: *Seler 2156* (CAS, US), *Seler 2238* (US; type collection of *H. Loesceneri*), *Matuda 2580* (NY, MICH), *Matuda 5183, 0404* (MICH). GUATEMALA—QUICHÉ: *Heyde & Lux 3034* (NY, US; type collection of *H. argenteus* var. *bifrons* Focke). HUEHUETENANGO: *E. Nelson 3666a* (US)), *Salas 470* (US). CHIMALTENANGO: *Hartweg 575* (NY). The specimen from San Juan Atitlán, Dept. Huehuetenango, *Skutch 1179* (NY), is very small-leaved, but the acute apex and the shape of the leaf would seem to place it with *H. fissus*.

8. HOLODISCUS ARGENTEUS (L.f.) Maxim., Acta Hort. Petrop. **6**: 254. 1879.

Slender shrub 1–5 m. high, branches drooping, often dependent, ribbed, older bark reddish-brown to dark gray, exfoliating, young twigs angled, gray-brown to tan, with a short, dense pubescence, often villous, internodes about half the length of the leaf, leaves in dense fascicles; leaf-blades oblanceolate to obovate, narrow cuneate at the base, decurrent on the petiole, the apex denticulate, rounded to round-obtuse, the lower three-fourths of the blade entire, the upper fourth denticulate, the teeth ending in a sharp, frequently bent mucro, 3–4 on each side, the leaf-blades glabrous to densely white-silky above, white-silky beneath, 1.5–3 cm. long, 0.5–1.5 cm. wide; petioles 1–3 mm. long; inflorescence sparse, spreading, usually narrow, densely villous-pubescent, 5–14 cm. long, 3–10 cm. wide; pedicels 2–3 mm. long, with 3 bracts, these lanceolate to broadly lanceolate, 1–3 mm. long; sepals broadly triangular-ovate with acute apex, 1.5–2 mm. long; petals oval to orbicular with a thick row of short, silky hairs along the back median line, extending to top of petal, more often with scattered pubescence on back, 2–3 mm. long; stamens as long as sepals; carpels villous, 2 mm. long; styles 1 mm. long, achenes often slightly curved on upper surface with a very convex lower surface.

Illustration: Figure 3.

KEY TO VARIETIES

Leaf-blades pubescent above.
  Leaf-blades equally white-silky above and beneath.
    Sepals with long dense pubescence. Colombia . 8a. *H. argenteus* var. *typicus.*
    Sepals with short matted pubescence. Chiapas, Mexico 8b. *argentus* var. *Matudai.*
  Leaf-blades with a very short pubescence above. Oaxaca, Mexico.
  8c. *H. argenteus* var. *velutinus.*
Leaf-blades glabrous to glabrescent above. Chimaltenango (Guatemala) and Costa Rica . . 8d. *H. argenteus* var. *alpestris.*

8a. H. ARGENTEUS var. **typicus** Ley, var. nov.

Spiraea argentea L. f. Suppl. 261. 1781; *Holodiscus argenteus* Maxim. Acta Hort. Petrop. 6: 254. 1879; *Schizonotus argenteus* Kuntze, Rev. Gen. 1: 225. 1891; *Sericotheca argentea* Rydb., N. Am. Fl. 22: 266. 1908; *Schizonotus argenteus* var. *Mutisianus* O. Kuntze, Rev. Gen. 1: 226. 1891.

Leaf-blades densely white-silky above and beneath; inflorescence 5–11 cm. long, 1–8 cm. wide, the pedicels with narrow lanceolate bracts, these 2–3 mm. long, rarely 1 mm. wide; petals with long, silky hairs along back of median line; sepals extremely villous with many long hairs.

TYPE collected by Mutis in Colombia, given as New Granada. Range, Colombia. *Material seen:* COLOMBIA—SANTANDER: *Killip & Smith 18477, 18179, 17254, 17430, 17310, 18576, 15795* (NY, US). BOYACÁ: *Cuatrecasas 1181, 1299* (US). CUNDINAMARCA: *Pennell 2095* (NY, US), *Cuatrecasas 5416* (US), *Holton 939* (NY), *Triana 4215* (NY, US), *André k 1006* (NY), *Schultze 31* (US), *André k 1007* (NY).

8b. H. ARGENTEUS var. **Matudai** Ley, var. nov.

Laminae foliorum in superficie superiore dense albido-sericeae, inferiore sericeae et villosae; inflorescentia parva, 3.5 cm. longa, 2 cm. lata; pedicellis cum bracteis lanceolatis, usque ad 2 mm. longis; petalis externe pubescentibus, sepalis cum pubescentia breve et densa.

TYPE: Mt. Tacaná, Chiapas, Mexico, *Matuda 2303* (NY; isotypes, MICH). Known only from the type collection.

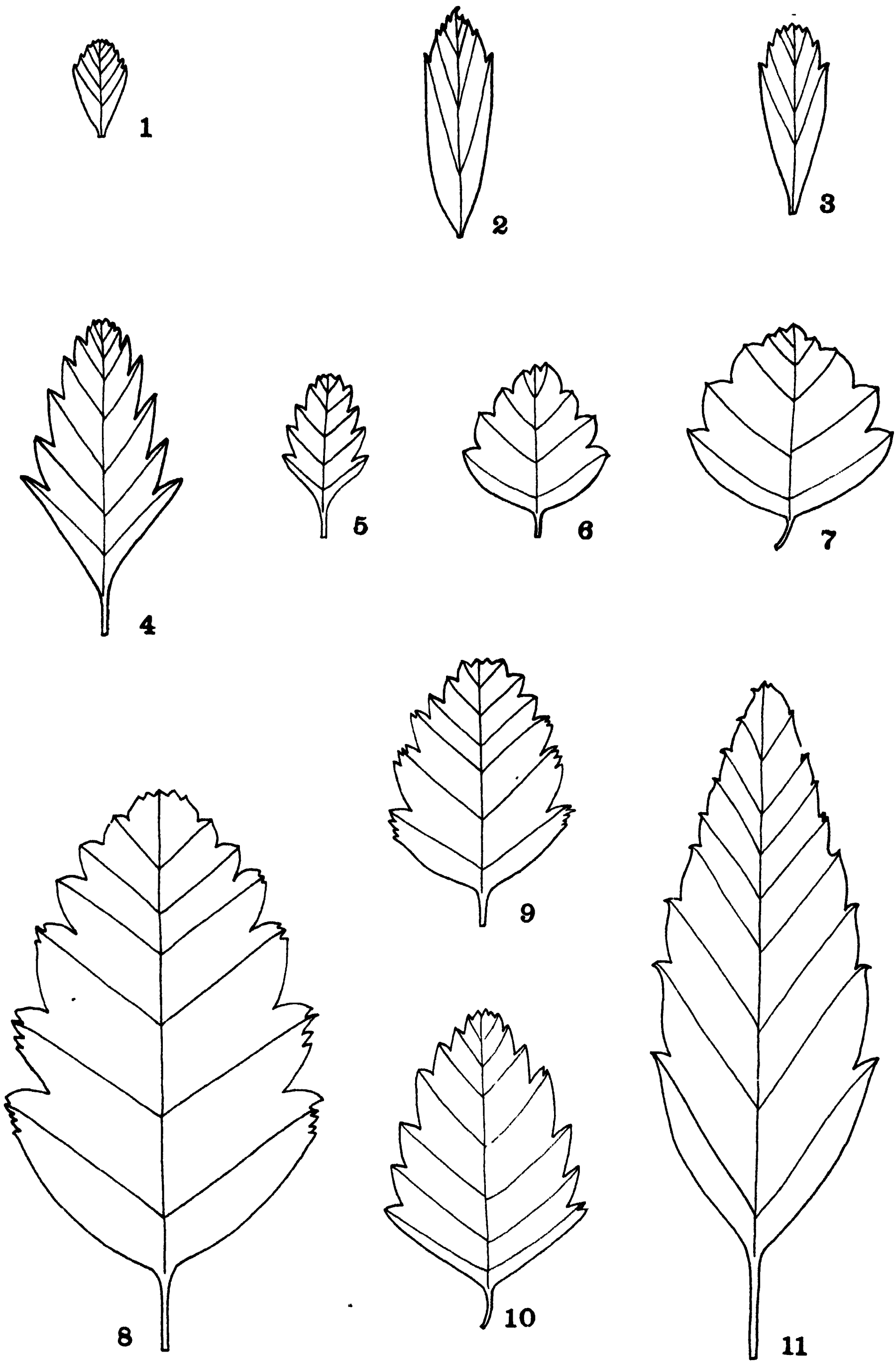
8c. H. ARGENTEUS var. **velutinus** (Rydb.) Ley, comb. nov.

Sericotheca velutina Rydb. N. Am. Fl. **22**: 265, 1908; *Holodiscus velutinus* Standley, Pub. Field Mus. Bot. 4: 210. 1929.

Leaf-blades with a very short, usually dense pubescence above, velvety; inflorescence over 7 cm. long, the pedicels with wide bracts, these broadly

Explanation of figures 1–11

Leaf shapes of the various species of Holodiscus. No shading nor pubescence is indicated. All drawings are made on the same scale; the length given includes blade and petiole. FIG. 1. *H. microphyllus.* Leaf 1.7 cm. long; Duran 3104. FIG. 2. *H. orizabae.* Leaf 2.9 cm. long; Liebmann 1670. FIG. 3. *H. argenteus.* Leaf 2.3 cm. long; Killip and Smith 17254. FIG. 4. *H. dumosus* var. *australis.* Leaf 3.7 cm. long; Wolf 2842. FIG. 5. *H. dumosus* var. *typicus.* Leaf 2.1 cm. long; Osterhout 2121. FIG. 6. *H. Boursieri.* Leaf 2.15 cm. long; Greene 1431. FIG. 7. *H. pachydiscus.* Leaf 2.8 cm. long; Bourgeau 267. FIG. 8. *H. discolor* var *typicus.* Leaf 7.1 cm. long; Thompson 9818. FIG. 9. *H. discolor* var. *franciscanus.* Leaf 4 cm. long; Santa Cruz Mts., San Mateo Co., Bond in 1928 (POM). FIG. 10. *H. discolor* var. *delnortensis.* Leaf 3.2 cm. long; Parks 24019. FIG. 11. *H. fissus.* Leaf 8.4 cm. long; Heyde and Lux 3034.


1
2
3
4
5
6
7
8
9
10
11

lanceolate and with acute apex, often 4 mm. long, 1 mm. wide; silky pubescence scattered over back of petal.

TYPE: Sierra de San Felipe, Oaxaca, Mexico, *Smith 821* (NY; isotype, US). Known only from the type locality. *Other material seen:* MEXICO—OAXACA: *Nelson 1085* (US).

Although this variety differs from var. *typicus* in lacking the silky appearance above, it does not seem to be sufficiently distinct to be made a separate species as Rydberg (op. cit.) does. The leaf size and shape, and the inflorescence are very like var. *typicus*.

8d. H. ARGENTEUS var. **alpestris** (Kuntze) Ley, comb. nov.

Schizonotus argenteus var. *alpestris* Kuntze, Rev. Gen. 1: 226. 1891.

Leaf-blades glabrous above; inflorescence 5–11 cm. long, 3–8 cm. wide, the pedicels with wide, lanceolate bracts, these 2–3 mm. long, up to 1 mm. wide; silky pubescence scattered over back of petal, particularly along veins.

Type locality, Irazú, Costa Rica, 3300 m. Range, Dept. Chimaltenango, Guatemala, and Costa Rica. *Material seen:* GUATEMALA—CHIMALTENANGO: *Standley 61842* (NY), *Skutch 430* (MICH, US), *Skutch 97* (US), *Seler 2361* (NY, POM, US). COSTA RICA—CARTAGO: *Herbarium of O. Kuntze 2358* (NY), *Pittier & Durand 187* (US), *Orsted 1668* (NY, US), *Pittier 14101* (US), *Niederlein* (US), *Stork 345* (US), *Rowlee & Stork 911* (NY, US). SAN JOSÉ: *Standley & Valerio 43555, 43962* (US). One specimen—plains near Tecpám, Dept. Chimaltenango, Guatemala, *Skutch 544* (US)—has an acute apex and conspicuous teeth, resembling *H. fissus;* however the small size and villous condition beneath would indicate it to be var. *alpestris*.

UNCERTAIN SPECIES

Spiraea mexicana Schiede, ined. 1835; Regel, Ind. Sem. Hort. Petrop. **1857**: 58. 1858. (*Schizonotus argenteus* var. *mexicanus* Kuntze, Rev. Gen. **1**: 226. 1891). The type of this species was not available, and the description is so short as to be of no aid in determining status. The country is given as unknown, but it would evidently be Mexican. Kuntze (l.c.) places the var. *mexicanus* in his key near to *Schizonotus argenteus* var. *fissus*. He does not cite specimens and consequently it is not known whether this specimen was accessible to him. Schneider (Handb. Laubh. **1**: 497. 1905) in his treatment of the genus cites this species as a synonym of *H. fissus*.

The following varietal names proposed by O. Kuntze, Rev. Gen. **1**: 225–6 (1891), in a key but without sufficient descriptions and without citation of specimens, are uncertain: *Schizonotus argenteus* var. *angustissimus*, may be *H. orizabae; S. argenteus* var. *griseus*, may be *H. dumosus* var. *Schaffneri; S. argenteus* var. *intermedius*, may be *H. pachydiscus*. Mexican and South American specimens were studied from both the United States National Herbarium and the New York Botanical Garden. None of this material could be identified as that upon which O. Kuntze based the above varieties. The Field Museum contained no material of *Holodiscus* collected by Kuntze. Since these three institutions are the only ones in this country known by me to have specimens of Kuntze's, it has been impossible to determine in which species Kuntze's varieties should be placed.

POMONA COLLEGE
CLAREMONT, CALIFORNIA

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 289–296 MAY, 1943

THE SECTION SEDASTRUM OF SEDUM[1]

ROBERT T. CLAUSEN

Sedastrum was first described as a genus by Rose in 1905 (N. Am. Flora **22**(1): 58). As basis for the generic status distinct from *Sedum*, Rose cited the dense basal rosettes of leaves, the numerous stems dying down to the base after flowering, the more or less paniculate inflorescences and the erect carpels concave under the scales. Berger (in Engl. & Prantl, Nat. Pfl. ed. 2. **18a**: 445. 1930) reduced the genus to the status of a section of *Sedum*, mentioning as characteristics the details already indicated by Rose, also the more or less fleshy, thickened rootstocks. Fröderström[2] designated *Sedastrum* as Group 10 of his Section *Americana Orthocarpia*. As diagnostic characteristics, he mentioned the usually pubescent, dense, *Sempervivum*-like basal rosettes, the paniculate inflorescences and the very thin, usually wavy petals.

The floral structure of *Sedastrum* seems sufficiently similar to the condition in *Sedum* to justify the continuance of this group of species in subgeneric rank rather than as a full genus. The vegetative characteristics which seem most important are the dense rosettes of leaves at the bases of the stems, the habit of the fertile shoots dying back to the base after flowering, and the thick rootstocks. The concavity of the carpels behind the scales, originally pointed out by Rose, perhaps is also important. As now understood, there are six species, all of which occur in Mexico, ranging from southern Coahuila to central Oaxaca.

The characters available for separating species of *Sedastrum* are mostly afforded by the vegetative structures—the habit of the plants, shape of leaves and pubescence. The flowers seem to be rather similar throughout the section, although the inflorescences vary considerably. The interpretation presented here is based largely on the examination of herbarium specimens, supplemented by study and observation of fresh plants, in cultivation, of four of the species. The present paper is not a final pronouncement on *Sedastrum*, but merely presents a summary of some of the available information and explains various names which I have used in identifying specimens. Before a final account of this section is possible, much more collecting and observation must be done in Mexico and careful cytological and genetical studies must be made.

The center of distribution for *Sedastrum* seems to be central Mexico, the area in which the largest number of species occurs. Differentiation seems to

[1] Studies in the Crassulaceae—IV.

[2] **Fröderström, Harold.** 1935. Group 10. *Sedastrum*. *In:* The genus *Sedum*, Part IV. Acta Hort. Got. **10**(Appendix): 72–79. *pl. 45–52.*

have developed from this center, but available data are insufficient at present to warrant speculation on the topic of phylogeny within the section.

In the following account, names of herbaria are abbreviated as: BH, Bailey Hortorium, Cornell University; CU, Department of Botany, Cornell University; NY, New York Botanical Garden; Pom, Pomona College; and US, United States National Herbarium.

KEY TO THE SPECIES OF SECTION SEDASTRUM

A. Flowering stems erect (sometimes short decumbent); plants glabrous or hairy ..... B
B. Plants glabrous or hairy, but never densely pubescent.
C. Leaves oblong, ovate or cordate ..... D
D. Plants large, ranging in height from 30–58 cm.; branches of inflorescence 2–30 cm. long ..... 1. *S. ebracteatum*
DD. Plants smaller, ranging in height from 15–30 cm. ..... E
E. Leaves thick, glabrous; carpels glandular ..... 2. *S. glabrum*
EE. Leaves thin, somewhat hairy; carpels smooth ..... 3. *S. chapalense*
CC. Leaves narrowly linear or oblanceolate ..... 6. *S. Hemsleyanum*
BB. Plants densely pubescent ..... 4. *S. Hintonii*
AA. Flowering stems procumbent or prostrate (sometimes hanging) ..... 5. *S. incertum*

1. SEDUM EBRACTEATUM A.P. DC. in Mém. sur la Fam. des Crassulacées, 37. *pl. 6, fig. B.* 1828. In the original diagnosis, the stem was described as tortuous and creeping at the base, with the flower-bearing part erect and the leaves glabrous. The figure shows a completely glabrous plant with thick fleshy oblong or ovate blunt leaves and with a much branched, paniculate cyme. A definite type locality was not designated. Both description and figure were obtained from Mocino's unpublished *Flore du Mexique.* Saunders (Ref. Bot. **4**: *pl. 221.* 1871) published a colored plate of this species with the basal leaves obovate, pale green and glabrous; and the stems glabrous. No pubescence appears in the colored plate except that the sepals seem to be ciliate. Hemsley (Diag. Pl. Nov. **1**: 11. 1878) redefined the species, apparently basing his conclusions on a cultivated plant in the herbarium at Kew. He stated that the species was poorly described by Saunders, but Saunders' description seems to check reasonably well with that of De Candolle. Hemsley described the leaves as oblong and white-pubescent and the cymes as spreading, also he wrote that the flowering branches are erect. Probably Hemsley had a specimen of a pubescent phase of the species, not an exact match for the plant illustrated by De Candolle.

Sedastrum ebracteatum (DC.) Rose, N. Am. Fl. **22**: 59. 1905.

Sedastrum rubricaule Rose, N. Am. Fl. **22**: 59. 1905. Based on plants collected by Dr. E. Palmer near Concepcion del Oro, State of Zacatecas, Mexico, Nov. 22, 1902 (*No. 386*). I have seen specimens from this collection. They are similar to the specimen figured by De Candolle. Like the type of the species they are almost glabrous and not to be regarded as varietally distinct on this basis.

Sedum rubricaule (Rose) Praeger, Jour. Roy. Hort. Soc. **46**: 132. 1921.

Sedum barrancae M. E. Jones, Contr. West. Bot. **18**: 37. 1935. I have seen the TYPE, which is *No. 191717* in the herbarium of Pomona College. It is the collection of M. E. Jones, *No. 27845,* Nov. 17, 1935, from wet loose soil

under cliffs at La Barranca, Guadaljara, Mexico. Jones did not mention how to distinguish his species *S. barrancae* from *S. ebracteatum*, *S. incertum* or any other species of *Sedum*.

Sedum ebracteatum var. *rubricaule* (Rose) Fröderström, Act. Hort. Bot. **10**(Append.): 73. 1935.

Tufted perennial with stems rigidly erect or short decumbent, 30–58 cm. high, glabrous or puberulent towards bases; rootstock fleshy-thickened, with fibrous roots and one or several dense rosettes of fleshy yellow-green leaves, obovate to ovate-elliptical, and either hairy or smooth; flowering stems green speckled with purple upwards, 8–10 mm. thick at base, 4–7 mm. thick just below inflorescence; cauline leaves oblong, oblong-lanceolate, elliptical or ovoid, blunt or acute, often clasping at base, 0.5–3.8 cm. long, 0.5–1.0 cm. wide, mostly reflexed and withered at time of flowering; inflorescence a lax, spreading paniculate cyme, with the branches 2–30 cm. long; flowers sessile, 5-merous; sepals green, oblong-ovate, obtuse, 2–3 mm. long, unequal; petals white with green median stripe dorsally, spreading or recurved, broadly oblong-ovate, 5–6 mm. long, united below; stamens 3-4 mm. long with filaments white and anthers pink; scales nearly square, about 1 mm.; carpels greenish, 4–6 mm. long, connate at base, with styles divaricate.

S. ebracteatum occurs under and about cliffs in central Mexico in the States of Hidalgo, Jalisco, Zacatecas and Durango. Specific altitudinal data are not available.

Specimens seen: northernmost—Concepcion del Oro, State of Zacatecas, *Edw. Palmer 386* (NY); easternmost—near Dublan, State of Hidalgo, *J. N. Rose & Robert Hay 218* (NY); westernmost—Guadalajara, State of Jalisco, *M. E. Jones 27845* (Pom); southernmost—same as westernmost; oldest—Nov. 22, 1902, Concepcion del Oro, *Edw. Palmer 386*. Number of collections seen—6.

Flowering time seems to be November.

Principal variations are in pubescence and habit. Some plants are glabrous, others are very pubescent. Likewise, the flowering stems may be erect from the base or procumbent.

S. ebracteatum is occasionally cultivated in greenhouses in temperate regions. Plants from cultivated sources have been correctly named.

2. Sedum glabrum (Rose) Praeger, Jour. Roy Hort. Soc. **46**: 127. 1921.

Sedastrum glabrum Rose, N. Am. Flora **22**: 59. Based on plants collected by Dr. E. Palmer at Saltillo in the State of Coahuila.

Perennial with stems erect or very short decumbent, 15–30 cm. high, usually glabrous throughout; rootstocks fleshy thickened, bearing one or several thick rosettes of fleshy, yellow-green, oblong, acute leaves which are convex dorsally, flat on the ventral face, 0.5–4 cm. long, 0.2–1.8 cm. wide and 0.2–0.7 cm. thick; flowering stem 2-6 mm. in diam. at base, 0.5–4 mm. in diam. just below inflorescence; cauline leaves oblong, acute, crowded, somewhat ascending at time of flowering, 0.2–2.7 cm. long, 0.1–0.9 cm. wide; inflorescence a paniculate cyme with the branches either ascending or recurved, 0.5–11 cm. long; floral bracts similar to the leaves, but markedly reduced upwards; flowers sessile or almost so; sepals green, oblong-ovate, obtuse, 2–3

mm. long; petals white, spreading, oblong-lanceolate, acute, 6 mm. long; stamens 4 mm. long; scales almost square, less than 1 mm., carpels greenish, 5 mm. long, glandular.

Known to me only from limestone hills near Saltillo, Coahuila (*E. Palmer 732* and other collections [NY]; and *C. G. Pringle 10090* [CU]), at an elevation of about 1830 m.; and from Santa María del Río, San Luis Potosí, *E. Palmer* (NY). The rosettes of the plants from San Luis Potosí are somewhat hairy. Number of collections seen—5.

The period of flowering seems to extend from July to September.

Sedum glabrum is rarely cultivated. From the horticultural trade I have received it as *Sedastrum Palmeri* (a manuscript name of Rose, used on herbarium labels and published in synonymy by Fröderström, Acta Hort. Göt. **10**(Appendix): 78. 1935). Plants cultivated at the New York Botanical Garden under another of Rose's manuscript names, *S. turgidum* (also published in synonymy by Fröderström, l.c.) are doubtfully to be referred here.

3. SEDUM CHAPALENSE S. Watson, Proc. Am. Acad. **22**: 411. 1887. Based on a specimen from Chapala, State of Jalisco, Mexico, collected by Dr. E. Palmer and preserved at the Gray Herbarium.
Sedastrum chapalense Rose, N. Am. Flora **22**: 59. 1905.

Perennial from a stout rootstock bearing one or several dense rosettes of obovate or ovate, acute, puberulent leaves; flowering stems 10–20 cm. high, glabrous, with the leaves ovate, acutish, 0.4–2.0 cm. long, puberulent; inflorescence a paniculate cyme with the branches more or less recurved and the sessile flowers densely crowded; sepals oblong-ovate, acutish, 2–3 mm. long, green; petals broadly oblong-ovate, acute, contracted towards the base, 5 mm. long, white; stamens 3–4 mm. long; nectar scales rounded at apex, broadest at base, about 0.5 mm. wide and 0.5 mm. long; pistils 5 mm. long, greenish, smooth.

Known at present only from the region of the type locality, Chapala, in the State of Jalisco, at an altitude of 1700 m. This species apparently is not cultivated.

When more collections are available, they may prove that *S. ebracteatum*, *S. glabrum* and *S. chapalense* are conspecific. Not enough material is now at hand to warrant such lumping, but the differences between these several so-called species seem relatively unimportant.

4. **Sedum Hintonii** Clausen, sp. nov. Figure 1. *Sedum*, sectionis *Sedastrum*, dense pubescens; rhizoma robusta prostrata, 5 mm. diam., rosulas densas ferens; folia rosularum congesta, anguste oblonga vel elliptica, 1.5–5 cm. longa et 0.3–1.0 cm. lata, apice obtuso, fulva quando sicca; caules floriferi ad 24 cm. alti, foliis lanceolatis, acutis, amplexicaulibus, 10–12 mm. longis, 4–5 mm. latis; inflorescentia cyma paniculata; ad 15 cm. longa, ramis late divaricatis; flores sessiles; sepalae 5, ellipticae-ovatae, obtusae, 2.5 mm. longae, 1.2 mm. latae; petalae 5, oblongae-lanceolatae, patentes, 4–5 mm. longae, 1.5 mm. latae; stamina 10, 2–4 mm. longa; squamae oblongae (fere quadratae), 0.3 mm. longae; carpella 5, 4 mm. longa; interius gibbosa, breviter connata ad basim, stylis gracilibus; semina rubra, subpyriforma, 0.7 mm. longa.

Perennial herb with prostrate stout rootstock, 5 mm. in diam., bearing slender roots and several dense rosettes; stems, leaves, branches of the inflorescence and sepals all densely pubescent with the hairs white, hyaline, mottled and somewhat flattened and stiff, to 1.5 mm. long; leaves of the rosettes crowded, narrowly oblong or elliptical, 1.5–5 cm. long, 0.3–1.0 cm. wide, obtuse at apex, yellowish brown when dried; flowering stems to 24 cm. high with the leaves lanceolate, acute, cordate clasping at base, 10–12 mm. long, 4–5 mm. wide; inflorescence a paniculate cyme to 15 cm. long with the branches widely spreading and the flowers crowded, and sessile, 3–10 on a branch; sepals 5, elliptical-ovate, obtuse, 2–2.5 mm. long, 1.2 mm. wide; petals 5, oblong-lanceolate, spreading, with crisped margins, 4–5 mm., 1.5 mm. wide; stamens 2–3 mm. long; nectar scales oblong (almost square), 0.3 mm. long; carpels 5, 4 mm. long, ventrally gibbous, briefly connate at base, with the styles slender; seeds red, subpyriform, 0.7 mm. long. Pinzan, 830 m., Coalcoman, State of Michoacan, April 13, 1941, *G. B. Hinton et al. 15926* (TYPE US *1808082*).

This species, known at present only from the type collection, differs from the other described Sedastrums in the abundant and peculiar pubescence, the flowers densely crowded on the branches of the inflorescence and the small lanceolate cauline leaves. It is probably nearest to *S. chapalense* and may be derived from that species. I am grateful to Mr. C. V. Morton, of the United States National Herbarium, for bringing to my attention Hinton's collection of the new species.

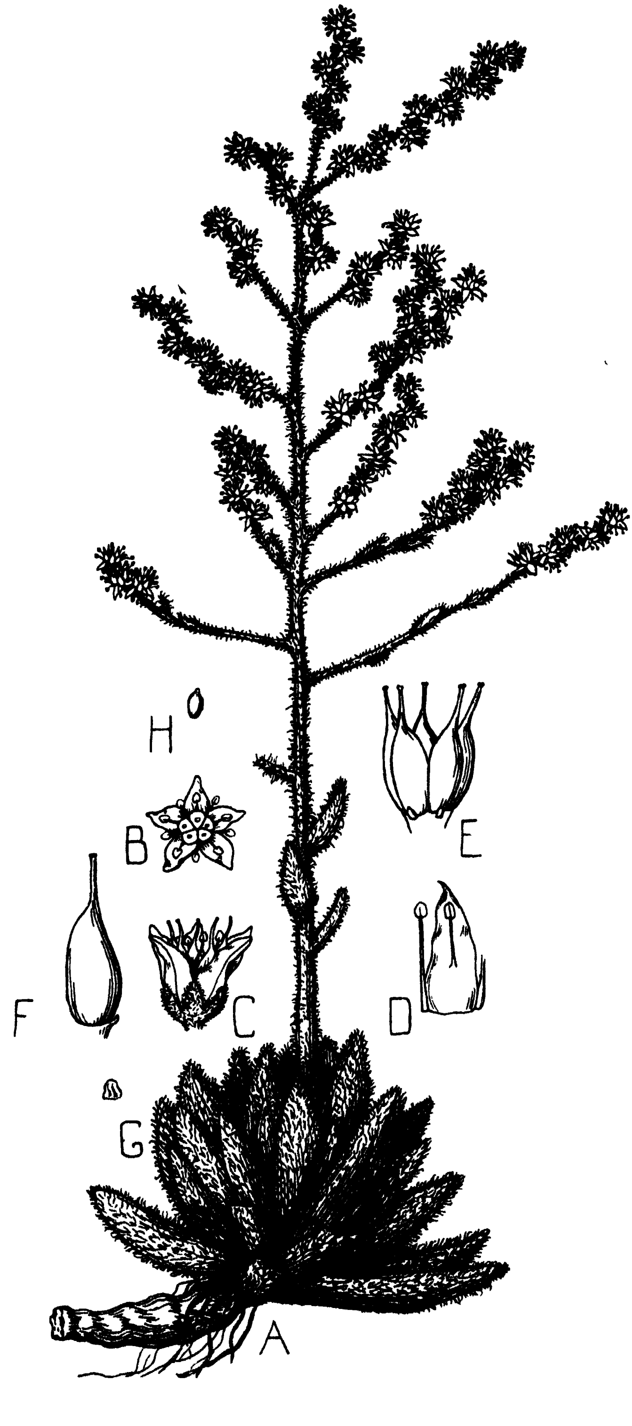
5. SEDUM INCERTUM Hemsley Diag. Pl. Nov. **1**: 11. 1878. The type in the herbarium at Kew has not been available to me. It is the collection of Bourgeau, *No. 1181*, from the Valley of Mexico. The original description seems reasonably clear: leaves fleshy, glabrous, broadly ovate or almost round, obtuse; flowers sessile in short congested cymes. This description fits rather well various specimens from Mexico.

Sedastrum incertum (Hemsley) Rose, N. Am. Fl. **22**: 59. 1905.

Lax perennial with stems procumbent or even hanging, glabrous or puberulent towards base; rootstock fleshy thickened, with fibrous roots and one or several dense rosettes of lustrous yellow-green fleshy leaves, ovate to oblong-elliptical and either glabrous or puberulent; stems 15–38 cm. high, 3–8 mm. thick at base, 1–3 mm. thick towards top; cauline leaves ovate, oblong-ovate, broadly elliptical or orbicular, blunt, often broadly rounded, 0.5–3.0 cm. long, 0.4–1.7 mm. wide; inflorescence a paniculate cyme with the individual branches of a single inflorescence usually less than 4 cm. long and bearing 1–6 flowers; flowers sessile, 5-merous; sepals green, oblong-ovate, obtuse, 2 mm. long; petals white, often with green median stripe, spreading or recurved, broadly oblong-ovate, 4–5 mm. long; stamens 5 mm. long with red anthers; scales subquadrate, about 1 mm.; carpels greenish, 4–5 mm. long.

S. incertum occurs on ledges and cliffs in central Mexico in the State of Hidalgo and the Federal District, probably also elsewhere.

Specimens seen:—northernmost—near Tula, 2068 m., State of Hidalgo, *C. G. Pringle 8693* (CU, NY); southernmost—cliffs above Guadalupe, Federal District, 2286 m., *C. G. Pringle 8693 1/2* (CU, NY). Number of collections seen—6.


H
B
E
F
C
D
G
A

Flowering time seems to be October and November. Cultivated plants, received as *S. incertum* and *S. ebracteatum,* flowered at Ithaca, N. Y., in December and January.

6. Sedum Hemsleyanum Rose, Bull. N. Y. Bot. Gard. **3**: 41. 1903. Based on three Mexican collections: *F. Muller 322* from Orizaba, *C. G. Pringle 6042* (TYPE) from near Oaxaca City, and *E. W. Nelson 2001* from between Petlacingo and Acatlan. I have examined representatives of all three collections.

Sedastrum Hemsleyanum Rose, N. Am. Fl. **22**: 58. 1905.

Sedastrum Painteri Rose, N. Am. Fl. **22**: 58. 1905. Based on plants collected near Cuernavaca, Mexico, and differing from *S. Hemsleyanum* primarily in being less pubescent and having oblanceolate cauline leaves. Specimens of the type collection impress me as being very similar to *S. Hemsleyanum* and not specifically distinct.

Sedastrum pachucense C. H. Thompson, in Trans. St. Louis Acad. **20**: 21. *pl. 10.* 1911. Based on plants collected at Pachuca in August, 1910. The illustrations accompanying the original description, depicting this species and *S. Hemsleyanum*, demonstrate the great similarity between the two. Praeger[3] has indicated the differences between them, but these impress me as relatively unimportant and not reliable.

Sedum pachucense Praeger, Jour. Roy. Hort. Soc. **46**: 128. 1921.

Sedum Painteri A. Berger, in Engl. & Prantl, Nat. Pfl. ed. 2. **18a**: 445. 1930.

Tufted perennial with stems erect or spreading, 10–26 cm. long, glabrous or pubescent; rootstock somewhat thickened, with several dense rosettes of spatulate, elliptical, or oblanceolate leaves, 0.5–1.0 cm. long, 0.1–0.3 cm. wide, blunt; cauline leaves, linear, narrowly elliptical or oblanceolate, usually terete or almost so, green or red, 3–20 mm. long, 0.5–4.5 mm. wide, acute or obtuse; inflorescence a paniculate cyme, 4–9 cm. long, with the branches 0.7–2.5 cm. long; sepals ovate-elliptical, acute or obtuse, 1.5–3 mm. long; petals white, oblong-lanceolate, 3–4 mm. long; stamens 2 mm. long; scales subquadrate, yellowish; carpels 4–5 mm. long, greenish white, with the styles slender to divergent.

S. Hemsleyanum grows on ledges and rocky banks at elevations of 1250–1700 mm. in the States of Hidalgo, Morelos, Oaxaca, Puebla and Vera Cruz.

Specimens seen:—highest altitude—1700 m., vicinity of Cuernavaca, State of Morelos, Dec. 1, 1932, *H. Fröderström & E. Hultén 536* (NY); lowest altitude—1250–1463 m., between Petlacingo and Acatlan, State of

Explanation of figure 1

Fig. 1. *Sedum Hintonii.* Drawings by Miss Julia Donaldson from the type collection. A. Habit sketch (× 0.7). B. Flower from above (× 2.25). C. Flower from side (× 2.25). D. Petal and two stamens (× 3.5). E. Carpels (× 3.5). F. Single carpel (× 4.5). G. Nectar scale (× 7). H. Seeds (× 7).

[3] **Praeger, R. L.** 1921. An account of the genus *Sedum* as found in cultivation. Jour. Roy. Hort. Soc. **46**: 1–314.

Puebla, Nov. 20, 1894, *E. W. Nelson 2001* (NY); northernmost—Pachuca, Hidalgo, the specimens described as *Sedastrum pachucense;* easternmost—Orizaba, Aug., 1853, *F. Müller* (NY); westernmost—same as lowest altitude; southernmost—near Oaxaca, State of Oaxaca, Nov. 12, 1894, *C. G. Pringle 6042* (NY); oldest—1853, Orizaba, *F. Müller*. Number of collections seen—12.

Flowering time, as determined from data with herbarium specimens, extends from September to December. Plants in cultivation in eastern United States usually flower in December and January.

S. Hemsleyanum differs in the degree of pubescence, the amount of red pigmentation and the relative acuteness or bluntness of the cauline leaves. Not enough specimens are yet available to demonstrate the degree of significance of these variations.

SUMMARY

Sedastrum is maintained as a section of *Sedum*. Six species are recognized, one of which, *S. Hintonii* from the State of Michoacan, is described as new. Four species, previously described, are relegated to synonymy.

DEPARTMENT OF BOTANY, CORNELL UNIVERSITY
ITHACA, NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 297–309 MAY, 1943

A PRELIMINARY INVESTIGATION OF THE NORTH AMERICAN CANES (ARUNDINARIA)

CHARLES L. GILLY

During the course of certain recent routine identifications, the problem of specific delimitation within the native canes of North America was again brought to my attention.[1] When the specimens in question were determined by means of the available keys to the genus there seemed to be scant question of their identity, for the differences given between *Arundinaria tecta* and *A. gigantea* (*A. macrosperma*)[2] seemed adequate for differentiation between the two species therein recognized. However, a subsequent comparison with material in the herbarium raised the question whether the differences given in the keys were really fundamental. From the preliminary examination of the available material it seemed that it would be advisable to make a further study in an attempt to ascertain if there might be differences, other than those of growth-habit, which could be used to separate unit-entities within the North American *Arundinaria* population.

A review of the literature on the native canes revealed that Brown has questioned the advisability of using the habital differences for specific delimitation.[3] Upon the basis of a study of material from Louisiana, he decided that only one species was present in that state; that it exhibited, under various conditions of growth, the two habital forms considered as typical of the two species (or species and variety) usually recognized. My study of the specimens available in the herbarium of the New York Botanical Garden supports Brown's contention so far as the Mississippi Valley and certain adjacent regions are concerned. However, an examination of specimens from the Atlantic Coastal Plain of Virginia and North Carolina leads me to believe that Brown was not justified in further assuming, on the basis of material from only one portion of the total distributional range, that all populations of *Arundinaria* in North America are to be included in a single species. It should be noted that Brown, like most others who have worked with North American *Arundinaria*, apparently did not consider the structural charac-

[1] "North America" as used throughout this paper excludes Mexico; the species of *Arundinaria* in that country and throughout Central America do not appear to be directly concerned in the present problem.

[2] The names *A. tecta* (Walt.) Muhl. and *A. gigantea* (Walt.) Chapm. are used for the two species recognized by Hitchcock (**Hitchcock, A. S.** 1935. Manual of the grasses of the United States, 29–30, 802–803). *A. macrosperma* Michx. is usually regarded as synonymous with *A. gigantea*, and is used instead of the latter name for the "large cane" of several of the current manuals.

[3] **Brown, C. A.** 1929. Notes on *Arundinaria*. Bull. Torrey Club **56**: 315–318.

ters of the spikelets; at least he makes no mention of these organs, other than to specify the manner of their arrangement in inflorescences.

A consideration of descriptions and keys in the currently available manual treatments of *Arundinaria*,[4] and of the original descriptions of the various specific or subspecific entities proposed in the North American segment of the genus, reveals one very surprising thing. Although the morphological characters of spikelets and florets are considered as providing the fundamental diagnostic characters for the classification of the grasses, these characters have almost never been utilized in studies of the native North American canes. Britton (l. c.) and Britton and Brown (l. c.) published the only American manual treatments in which the spikelets have been considered much beyond the fact that they are sometimes present on the plants. Even here the spikelets were given no real emphasis, and were not used in the differentiation of the species recognized by these authors. Ruprecht and Munro, European students of the Bambuseae, considered the characters of the spikelets in some detail.[5] The former utilized spikelet differences to separate varieties of *A. tecta*, and the latter mentioned certain of these differences but rejected them on the basis of apparent "intermediates" available to him.

It is pertinent to this discussion to note that the specimens from which the illustrations of *A. gigantea* and *A. tecta* in Hitchcock's Manual (l. c., figs. 1 and 2) were drawn both came from Virginia (*Chase 5880* and *5881*). Although I have not seen these particular specimens, the illustration of *A. tecta* agrees exceedingly well with a specimen collected in Virginia by Mrs. Chase, and widely distributed as *Amer. Gr. Nat. Herb. no. 498*. The dimensions of the spikelets as illustrated for *A. gigantea* indicate that they are quite similar to those illustrated for *A. tecta*. When the spikelets of the Chase specimen from Virginia were compared with those of *Brown 4018* (the only specimen from Louisiana available to me), certain rather striking differences, which appeared to merit further consideration, were observed.

[4] **Britton, N. L.** 1901. Manual of the flora of the Northern States and Canada, 185. In subsequent editions the treatment of *Arundinaria* is unchanged. **Britton, N. L., & Brown, A.** 1913. An illustrated flora of the Northern United States, Canada and the British Possessions. ed. 2. **1**: 295. **Hitchcock, A. S.** 1935. Manual of the grasses of the United States, 29, 30. **Robinson, B. L. & Fernald, M. L.** 1908. A handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada [Grays' New Manual of Botany, Edition 7], 1–171. **Small, J. K.** 1933. Manual of the Southeastern Flora, 138, 139.

[5] **Ruprecht, F. J.** 1839. Bambuseae. [separate from] Act. Acad. Caes. Petrop. VI. 5(2): 1–74. *pl. 1–18*. This was reprinted with different pagination early in the following year; the correct citation of this second issue, according to data published by P. L. Ricker (Proc. Biol. Soc. Wash. **21**: 11–18. 1901.), is as follows: Mem. Acad. St. Petersb. **5**(2; Sc. Nat. **3**): 91–165. *pl. 1–18*. 1840. Hitchcock (l. c.) has used essentially this last citation in the listing of certain Ruprecht names, but has erroneously given the date as of the earlier extract. **Munro, Col. W.** 1868. A monograph of the Bambuseae, including descriptions of all species. Trans. Linn. Soc. **26**: 1–157.

The next step in this preliminary study was to sort all available spikelet-bearing specimens of North American *Arundinaria* into two groups, using the spikelet characters of the Chase and the Brown specimens as criteria for this sorting. Most of the specimens examined could easily be referred to one or the other of the two groups, but a few were apparently intermediate in varying degrees; these "intermediates" will be more fully discussed in a later paragraph. It was discovered, when the sorting of specimens had been completed, that those with spikelets similar to those of the Chase specimen were almost entirely restricted in distribution to the Atlantic Coastal Plain (see map, fig. 1). For subsequent discussion these will be considered as constituting the *atlantic-type* of North American *Arundinaria*. The specimens with spikelets similar to those of the Brown specimen—although they collectively occupy a much wider distributional area than the name would imply—will be referred to as the *mississippi-type*, because this appears to be the only sort of spikelet represented in the cane populations of the Mississippi Valley.[6] These two spikelet types may be characterized as follows:

Mississippi-type: Spikelets 5–8(–10)-flowered, 3.5–5(–7) cm. long; lemmas green or greenish, densely pubescent or rarely glabrescent in age, with conspicuous transverse thickenings between the nerves, the lower and median lemmas 1.5–2.75 cm. long, tapering to an acuminate, long-acuminate, or subaristate apex; inner glume one-half or slightly less than one-half the length of the lemmas, greenish, pubescent, acute at the apex, the median one of the several equally prominent nerves reaching the apex; outer glume similar to the inner but smaller (figure 2, M1–M4; localities where specimens with this sort of spikelets have been collected are indicated on map, fig. 1, as black disks).

Atlantic-type: Spikelets 5–10(–12)-flowered, 2–4 cm. long; lemmas purple or purplish-tinged, glabrous except for minute marginal ciliation toward the apex, transverse thickenings not visible between the nerves, the lower and median lemmas 0.8–1.5 cm. long, their apices merely acute or somewhat rounded; inner glume never more than one-third the length of the lemmas, purple or purplish, glabrous except for sparse ciliation at the blunt or truncate and generally erose apex, the mid-nerve rarely reaching the apex and the lateral nerves obscure or obsolete; outer glume similar to the inner but much smaller or sometimes lacking (fig. 2, A1–A4; localities where specimens with this sort of spikelets have been collected are indicated on map, figure 1, as black triangles).

From this preliminary study there also appears to be a correlation between type of spikelet and type of leaf sheath in the specimens which I have examined where both spikelets and foliage were present. The type of leaf

[6] Extensive field studies of the North American cane population may perhaps necessitate a future modification of this statement; on the basis of the specimens available to me, there is no evidence of the presence of the *atlantic-type* west of Biloxi, Mississippi, from which locality I have seen an apparently "intermediate" specimen which can be considered as *atlantioid* in spikelet-type.

sheath (fig. 2, M5), which appears to be correlated with *mississippi-type* spikelets, has a densely and conspicuously pubescent exterior-ligule, and the clusters of auricular bristles at either side of the apex of the sheath are more or less united at the base into a triangular wedge of tissue distinctly different in color and texture from the sheath region immediately below. The individual bristles are larger in diameter and more coarsely scabrous than in the *atlantic-type* sheath. In this latter type of sheath (fig. 2, A5) the groups of bristles are not basally united above the apex of the leaf sheath,

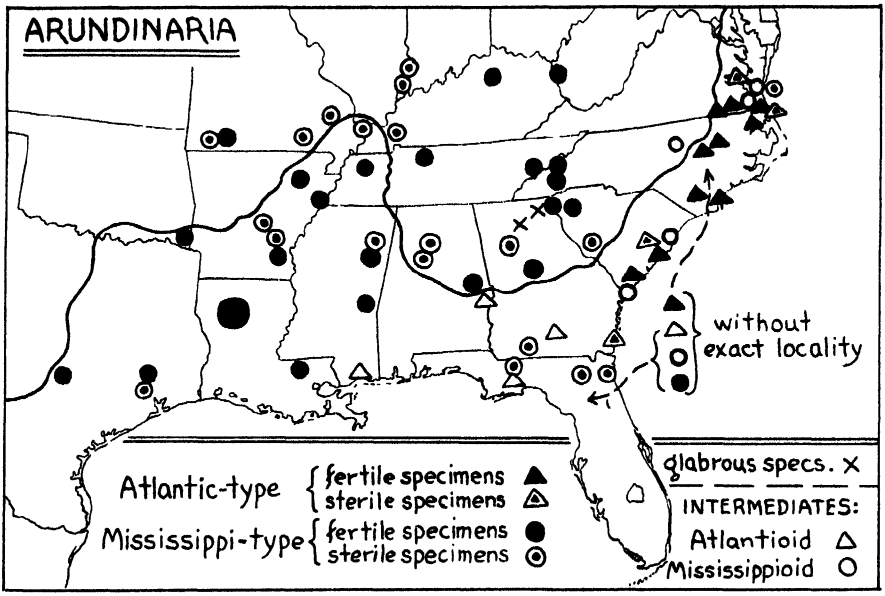


FIG. 1. Distribution of *Arundinaria*, based on specimens in the herbarium of the New York Botanical Garden. The inner boundary of the Coastal Plain is approximately indicated by a heavy line. Some of the symbols on the map represent more than one collection from the same or closely adjacent localities. Illustrations of the spikelet and leaf sheath characters which form the basis of the two types recognized within the genus are presented in figure 2. The localities of two collections, mentioned in the text as being vegetatively glabrous and having somewhat different leaf sheath characters, are indicated by the symbol ×.

and the exterior-ligule is either glabrous or microscopically ciliate. The interior-ligules of both types are variable, although the *mississippi-type* appears to be always more or less pubescent while the *atlantic-type* is either glabrous or sparsely ciliate with bristle-like hairs. The overlapping margin of the sheath proper is either glabrous or minutely pubescent in the *atlantic-type,* while in the *mississippi-type* it is usually coarsely ciliate.

It is perhaps of more than casual interest to note that in the available specimens of South American and Central American *Arundinaria* and *Arthrostylidium* (a closely-related and perhaps not adequately separable

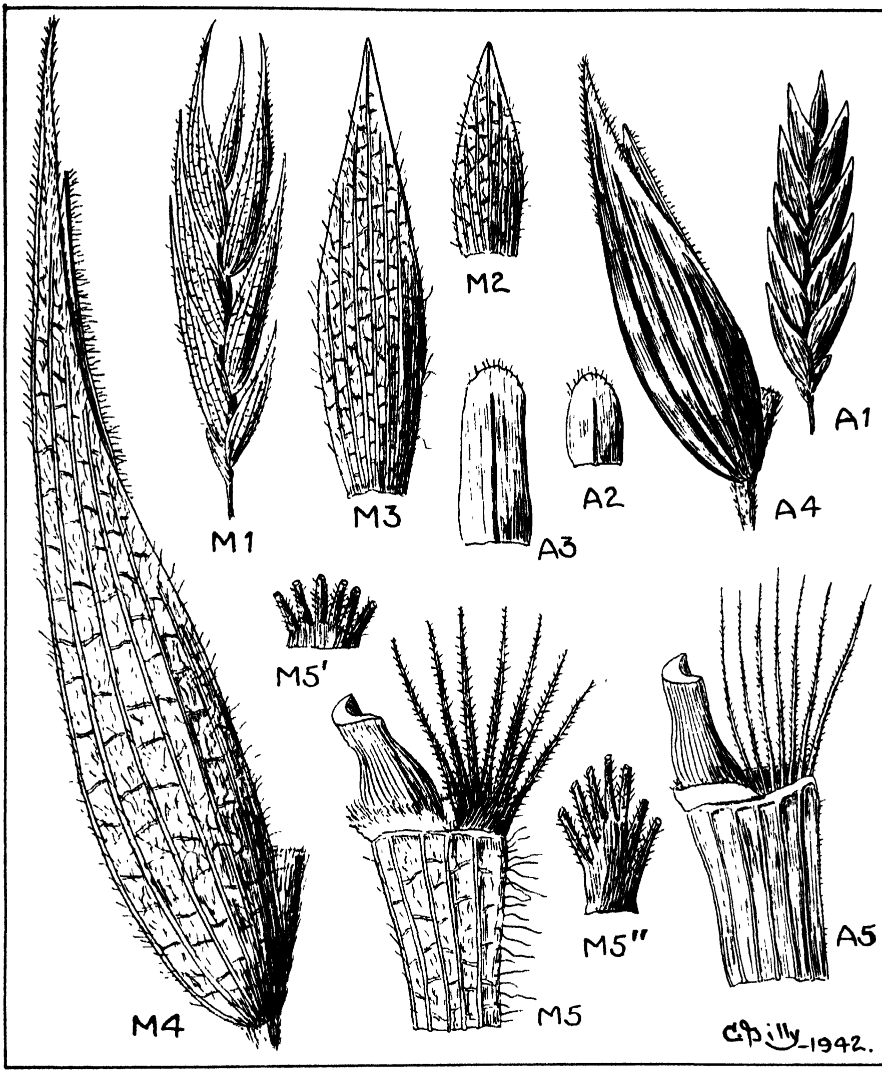


FIG. 2. Morphological characteristics of the two types of *Arundinaria* in North America north of Mexico. A1–A5: the *atlantic-type;* M1–M5: the *mississippi-type*. Portions of the plants illustrated are: 1. spikelets (× 1.5); 2. outer glume (× 6); 3. inner glume (× 6); 4. lemma (× 6); 5. apex of leaf sheath (× 3). Figures A1–A4 were drawn from *Fernald and Long 6940*, from near Crismond, Nansemond Co., Virginia, and figure A5 from *A. Chase s. n.* (*Amer. Gr. Nat. Herb. no. 500*) from the Back Bay section of Princess Anne Co., Virginia. Figures M1–M4 were drawn from *Bush 198*, from Eagle Rock, Barry Co., Missouri, and figure M5 from *Gattinger s. n.* (*Curtiss' N. Am. Pl. Distrib. no. 3523*) from near Nashville, Tennessee. The range of variability in the degree of basal fusion of the auricular bristles from the *mississippi-type* leaf sheath is indicated in figures M5′ (drawn from *Demaree 13950*, from Jefferson Co., Arkansas) and M5″ (drawn from *Combs 149*, from near Lake City, Columbia Co., Florida); only the basal portion of the cluster of auricular bristles is shown in these last two figures.

genus of the Western Hemisphere) the leaf-sheath apices and auricular bristles are like those of the *atlantic-type*,[7] while in specimens which I have examined from eastern Asia the bristles and sheath-apices are like those of the *mississippi-type*. It seems safe, here, to postulate that this latter type of leaf sheath is characteristic of a Holarctic group of species, the North American segment of which is now disjunct from the Asiatic. The *atlantic-type* of leaf sheath, closely similar in structure to the South American type, is indicative of the relationship of this type of *Arundinaria* with the South American members of the genus.[8]

Specimens apparently intermediate between the *atlantic-type* and *mississippi-type* have already been briefly mentioned. These "intermediates" are of several sorts. In some of them, the characters of the two types of spikelets are combined in varying degrees. In others where both spikelets and foliage are present, some association of *atlantic-type* spikelets with *mississippi-type* leaf sheaths (and vice versa) was evident; also a few of the sterile specimens examined seemed to combine the characters of both types of leaf sheaths. These intermediates are indicated on the accompanying map (fig. 1) by either white triangles or circles, dependent upon the degree in which they seem to approximate one or the other of the two types.

A consideration of the accompanying map (fig. 1) reveals that while the *mississippi-type* is common through the lower Mississippi Valley and on the Gulf Coastal Plain, it is also more or less widely distributed through portions of the two old land masses of eastern North America—the Ozark area and the Appalachian-Cumberland region. The *mississippi-type*, therefore, appears to represent a North American species whose affinities, as already men-

[7] This is particularly apparent in certain as yet unidentified specimens from Honduras (*Yuncker, Dawson & Youse 6085*) and Central Brazil (*Krukoff 7273*) as well as in material identified as *Arundinaria deflexa* E. E. Br. from the summit of Mt. Roraima on the British Guiana–Venezuela–Brazil boundary corner. This latter species, although apparently exhibiting the growth-habit of North American *Arundinaria*, seems to have spikelets approaching those of *Arthrostylidium* in flower number. The sheet of *A. deflexa* (*Tate 471*) in the herbarium of the New York Botanical Garden is sterile, and I know the spikelets of this species only from the original description (**Brown, N. E.** *et al.* 1901. Report on two botanical collections made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Trans. Linn. Soc. II **6**: 1–109). *Arthrostylidium* appears to represent a further development of several reductionary trends than does *Arundinaria;* these are a decrease in flower number per spikelet, the elimination of sheath bristles in some species, and the acquisition of an herbaceous or a liana habit of growth. Various workers with the Bambuseae have either included *Arthrostylidium* in *Arundinaria*, or have considered it as a closely related genus. Further study of this Caribbean and South American genus may perhaps be essential to the ultimate solution of the problems of the North American *Arundinaria*-complex.

[8] For a discussion of a similar relationship in another plant group, a recent paper in which the North American species of *Gaylussacia* are considered should be consulted (**Camp, W. H.** 1941. Studies in the Ericales: A review of the North American Gaylussacieae; with remarks on the origin and migration of the group. Bull. Torrey Club **68**: 531–551).

tioned are with the species of eastern Asia. Its present much wider distribution is almost certainly due to a migration into the Mississippi-embayment and Coastal Plain as these related areas became available for colonization by plants.[9] The *atlantic-type*, on the other hand, is largely restricted to the Atlantic Coastal Plain although *atlantioid* individuals have been collected in the eastern segment of the Gulf Coastal Plain.

The presence of *mississippioid* individuals on the Atlantic Coastal Plain seems entirely due to a downward and outward migration of this species from the Appalachian upland areas. In the northern-part of the distribution area of the genus this migration would seem to have been along ancient drainage systems.[10] Further south (in South Carolina and Georgia) where *mississippioid* individuals occur, this migration is undoubtedly continuing today. It is to be expected that in at least some of the Atlantic Coastal Plain localities where the *mississippioid* individuals are known, that colonies of the *mississippi-type* may be found; the frequency and extent of these colonies will, in part, depend upon the degree to which this type has been genetically submerged by the *atlantic-type*.

So far as vegetative characters, other than those of the distal portion of the leaf sheath, are concerned, I have been unable to find any correlation with either type of spikelet—except perhaps as regards leaf shape. Leaf size appears to be extremely variable in the series of specimens assigned to both the *atlantic-type* and the *mississippi-type*. Most individuals of the former type, however, seem to have a lanceolate-acuminate leaf blade in contrast to the merely acute and narrowly lanceolate-elliptic leaves present in most individuals of the latter type.

[9] Dr. W. H. Camp informs me that he has seen "cane" growing abundantly in parts of Kentucky and eastern Tennessee, in both states often on hillsides where the forest cover was not too dense. From his description of these areas it is apparent that the habitat is similar to that of various of the *Arundinaria* species in eastern Asia; and, as is well known, these areas of the southeastern United States contain numerous species in other genera and families which have cognate forms in eastern Asia. It is therefore likely that the populations of the *mississippi-type*, so common along the larger streams and rivers, may have been entirely derived from just such hillside populations as those now growing near the heads of the present drainage systems.

[10] Although *Arundinaria* is reported as ranging northward in the interior as far as Highland County, Ohio, and along the coast to New Castle County, Delaware, and Anne Arundel County, Maryland, I have seen no specimens from these localities. It is quite probable that before the Pleistocene the *mississippi-type* had a much more northerly distribution in the Appalachian-Cumberland region. Evidence which seems to support this statement is found in a report of the finding of half-masticated portions of plants of "a species of Arundo, or Arundinaria, still common in Virginia" in the well-preserved stomach of a mastodon (*Mammut americanum*) whose skeleton was discovered in Wythe County, Virginia, in 1806 (**Hay, O. P.** 1914. The Pleistocene mammals of Iowa. Rept. Iowa Geol. Survey **23**(1912); in particular, p. 367 of the section dealing with the food of the mastodon). Rearrangements in the drainage pattern—these, in part, occurring in pre-Pleistocene times—in the region which now includes North Carolina, Virginia, West Virginia, Maryland, and Pennsylvania have perhaps prevented subsequent coast-ward migration of the *mississippi-type* in this area.

Although pubescence of leaf blades and sheaths appears to be variable in individuals of both types, there are a few more or less isolated populations which appear to have always been glabrous; this characteristic is best shown by two collections made by J. K. Small in Georgia, one on the Yellow River in Gwinnett Co. (July 20, 1893), the other in Habersham Co., between Toccoa Falls and Tallulah Falls (Sept. 3, 1894). These particular specimens, both in their glabrous nature and somewhat different leaf sheath characters, are very similar to certain species of *Arundinaria* from eastern Asia. Whether they represent a disjunct remnant of a species or species-complex with a formerly wide Holarctic distribution, or whether these specimens may have been collected from naturalized colonies of one of these East Asian species, can not be decided on the basis of the evidence at present available to me. Further study of the cane populations in these areas will be necessary to clear up this particular point.

Another point, regarding certain Alabama populations of *Arundinaria* described by Harper, also appears to need further investigation.[11] In contrast to Brown's conclusions from a study of Louisiana canebrakes, Harper—after a study of Alabama populations of *Arundinaria*—stated: "This genus is not very fully understood, partly on account of the scarcity of flowers and seeds, and the number of species in North America may be anywhere from one to three or four. In Alabama there seem to be two, or possibly three." Although Harper gave few differences between the species except comparative height, culm diameter and frequency of flowering, he definitely recognized two species as present in Alabama.

A. macrosperma, found "on river banks and in creek swamps, a little below high-water mark," was said to be distributed essentially throughout the state except in the Blue Ridge, Piedmont, and Outer Coastal Plain portions of Alabama. *A. tecta*, which "grows mostly in sandy bogs, wet woods and non-alluvial swamps, south of the coal regions," was listed as occurring in the Blue Ridge and Piedmont areas, and as particularly common through the Outer Coastal Plain. According to Harper this second species had not been found in the northwestern one-fourth of the state. At the end of his discussion of *A. macrosperma* he remarks: "What may be another species, resembling *A. macrosperma* except in size (being smaller) and habitat, grows on sandstone, shale and limestone cliffs in various parts of the state as follows: 1B. On limestone mountain slopes, within a few miles of the Tennessee River in Jackson, Madison and Marshall Counties. 2B. Bluffs near Simpson's Creek, Cullman County. Cliffs near Warrior River, Walker and Tuscaloosa Counties. 3. Near Sylacauga. 11. Hatchetigbee Bluff on Tombig-

[11] **Harper, R. M.** 1928. Economic Botany of Alabama. Part 2. Catalogue of the trees, shrubs and vines of Alabama with their economic properties and local distribution. Geol. Survey Alabama, Monograph 9; in particular, pp. 72–77, *figs. 18–20*.

bee River, Washington County."[12] Although I have examined a number of specimens collected by Harper in Alabama, there are apparently no examples of this upland type of *Arundinaria* in the herbarium of the New York Botanical Garden. The habitat, as given by Harper, is strikingly reminiscent of that of certain Eastern Asiatic species of the genus.

Before briefly discussing the nomenclatural aspect of the problem of the North American canes, it seems necessary to give some consideration to the habital differences which have so long been considered as indicative of specific distinctness. A quotation from Mohr[13] clearly presents these habital differences:

"*Arundinaria tecta* rarely exceeds the height of 12 to 15 feet, and the slender culm branched from the base is seldom half an inch in thickness. Early in spring, apparently every three or four years, the paniculate flowers are produced on naked[14] radical shoots scarcely exceeding 18 inches in height, while the tall flowerless canes are sent up every season from the long creeping rhizomes. *Arundinaria macrosperma*, from 15 to 30 ft. high and frequently an inch and over in diameter, produces the panicles of its flowers in the axils of the branches at long and indefinite intervals of time. . . . The seedlings [of *A. macrosperma*] produce no branches during the first year. These simple shoots, which are known as 'mutton cane' are tender and sweet and afford the best of pasturage."

In regard to the habital characteristics and different modes of flower production, Brown (l. c., pp. 316 and 317) has made the following observations:

"Spikelets of *Arundinaria* were first collected by the writer in March, 1927, in a canebrake near Baton Rouge, Louisiana (*no. 989*). These were from the lower nodes of old canes that had been cut off one or two joints above the ground. In November, 1927, a considerable portion of the canebrake in which the above specimens were collected was cleared. During the last of March and April, 1928, flowers were again found on the lower nodes of the cane stubble. . . . About the first of May there appeared in the same field a large number of somewhat shrubby radical shoots which bore terminal panicles, and according to the manuals should be *A. tecta*. . . . In one of the places where the cane was found in bloom a drainage ditch had been dug in the early part of January, 1928. In this place, flowers were found on both radical shoots and on the old canes. On digging up some of the plants, it was

[12] The numerical designations (1B, 2B, 3, and 11) in the above quotation refer to "natural regions" of Alabama as delimited on map 1, page 33, of Harper's publication.

[13] **Mohr, C.** 1901. Plant Life of Alabama. Contr. U. S. Nat. Herb. **6**. pp. 921. Washington, D. C. Later in the same year this volume was reprinted with identical pagination and issued as a publication of the Geologic Survey of Alabama. The quotation given here is from page 103.

[14] By "naked" Mohr evidently meant the absence of leaves with "blades." The available specimens and illustrations of the "*tectoid*" phase of the cane populations indicate that the culm of the radical shoot is closely covered by overlapping bladeless, or essentially bladeless, sheaths. The specific epithet of Walter's *Arundo tecta*, on which *Arundinaria tecta* is based, is indicative of this character, for it is derived from the latin *tectus*, meaning enclosed or covered.

found that some of the radical shoots with flowers (*A. tecta*) came from the same rootstock as did stalks with lateral spikelets (*A. macrosperma*). . . . A careful examination of several other canebrakes in flower during the spring of 1929 has resulted in finding flowering radical shoots attached to the same rootstock as the old flowering canes. One collection (*no. 2435*) was made near Erwinville, Louisiana, on the edge of a thicket which had not been cut or drained for several years. This suggested that both forms of *Arundinaria* may occur on the same rootstock naturally and that cutting or some other stimulation may not be necessary."

Some of the specimens of the *mississippi-type* which I have examined are clearly from the leafless, sheath-covered radical shoots of the growth-form commonly called *A. tecta*. On the basis of the specimens which I have examined and referred to the *atlantic-type,* it is apparent that tall canes with complexly branched axillary inflorescences and the low radical shoots with terminal inflorescences are both present in this segment of *Arundinaria* as well as in the *mississippi-type* segment. The consecutive collection numbers (*5880* and *5881*) of the Chase specimens from Virginia—previously mentioned as being the basis for the Hitchcock manual illustrations of *A. gigantea* and *A. tecta*—suggests that these two specimens might have been collected from a single Virginia canebrake. If so, they would seem to represent a condition parallel to that observed by Brown in certain Louisiana canebrakes.

Although two distinct types of spikelets are present in the North American *Arundinaria* populations—and these being representative of unit-entities which in all probability are worthy of specific rank—a definite application of names to these entities is not yet possible because the present concepts within the group are based primarily on habital differences.[15] The final solution of the nomenclatural phase of the problem must await (1) a more complete understanding of the variability and complexity of populations within

[15] In future work on the nomenclatural phases of the North American *Arundinaria* problem, it will be necessary to consider (in addition to those already cited in this paper) at least the following publications, all of which have been consulted during the preparation of this preliminary paper: **Camus, E. G.** 1913. Les Bambusées. 1–215. **Chapman, A. W.** 1860. Flora of the Southern United States; in particular, pp. 561 and 562. **Elliott, S.** 1816–1821. A sketch of the botany of South-Carolina and Georgia. Vol. 1; in particular, pp. 96 and 97. **Hitchcock, A. S.** 1905. The identification of Walter's grasses. Rep. Mo. Bot. Gard. **16**: 31–56. 1908. Types of American grasses; A study of the American species of grasses described by Linnaeus, Gronovius, Sloane, Swartz, and Michaux. Contr. U. S. Nat. Herb. **12**: 113–158. 1920. The Genera of Grasses of the United States, with Special Reference to the Economic Species. U. S. Dept. Agric. Bull. **772**; in particular, pp. 22–24. **Michaux, A.** 1803. Flora Boreali-Americana. **1**: 73–74. **Muhlenberg, D. H.** 1817. Descriptio uberior Graminum Plantarum Calamariarum Americæ Septentrionalis Indigenarum et Cicurum; in particular, pp. 191 and 192. **Nuttall, T.** 1818. The genera of North American plants, and a catalogue of the species to the year 1817. **1**: 39. 1837 Collections towards a flora of the Territory of Arkansas. Trans. Am. Phil. Soc. II. **5**: 139–203. **Walter, T.** 1788. Flora Caroliniana; in particular, p. 81.

the genus, and (2) the reexamination of the Walter and Michaux type specimens, now in European herbaria, to determine whether or not the names based on these specimens can be definitely referred to either the *atlantic-type* or the *mississippi-type* of North American *Arundinaria.*

Pending an examination of the existent type specimens, it will be necessary to refer to these two types of *Arundinaria* by names of some sort. It is my suggestion, if the designations *atlantic-type* and *mississippi-type* do not seem to be adequate for this purpose, that the two oldest names seemingly referable on a geographical basis to these two types, be used. The *atlantic-type*, then, could be temporarily referred to as *A. gigantea*, and the *mississippi-type* as *A. macrosperma.* The name *A. tecta*—because no specimen of *Arundo tecta* (on which *Arundinaria tecta* is based) is in the Walter herbarium, and because of the presence of "*tectoid*" phases in both the *atlantic-type* and the *mississippi-type*—should, for the time being, be considered a *nomen dubium.*[16]

In the event that the Walter specimen of *Arundo gigantea* proves to be in such condition that it can not be surely referred to either the *atlantic-* or the *mississippi-type* of *Arundinaria*, I would recommend that the varietal epithet *colorata* of Ruprecht (l. c., p. 22) be raised to specific rank for the *atlantic-type* to which, on the basis of description and accompanying illustration, it is clearly referable. This procedure can, however, be followed only if the type specimen of *A. macrosperma* is definitely determined to be of the *mississippi-type.*[17] Should this specimen prove either to be unidentifiable or of the *atlantic-type*, the only available specific epithet for the *mississippi-type* populations would be Nuttall's *pumila*, for there can be no question as to which type of *Arundinaria* Nuttall was considering when he described *Miegia pumila* (1837, l. c.). However, because of the size connotation, perhaps it would seem to be somewhat unfortunate if it should be necessary to apply this epithet to the predominantly tall canes of the *mississippi-type.*[18]

[16] According to Hitchcock (1905, l. c.) the type of *Arundo gigantea* in the Walter herbarium (in the British Museum) consists merely of a sterile shoot with two leaves; no specimen of *Arundo tecta* is present in the Walter collection. Also, Hitchcock (1908, l. c.) states that the Michaux specimen (in the Muséum d'Histoire Naturelle at Paris) of *Arundinaria macrosperma* is fragmentary and difficult to assign to either of the two species; this last statement is almost certainly made on the basis of habital characters only.

[17] From the wording of the distributional statement accompanying the original description—"*HAB.* ad ripas flum. Mississipi: in Carolina, Florida, &c." (Michaux, l. c.)—it would appear that Michaux collected the type of the species somewhere on the Mississippi River. However, Hitchcock (1908, l. c.) records the data on the label of the type specimen as follows: "Gramen altissimum ramosum a Virginia ad Floridam & in occidentalibus juxta fluviis ad Illinoensibus ad ostium Misissipi." This is suggestive that Michaux's specimen came from somewhere on the Atlantic Coastal Plain.

[18] Actually, the use of this epithet might not be really so unfortunate. If, as is previously intimated in this paper, the lowland populations of the *mississippi-type* have been derived from the upland types now present at the headwaters of certain of the tributaries of the Cumberland-Appalachian drainage systems, then these coarse canes might well be

There perhaps may be some question why I did not borrow and examine all of the specimens of *Arundinaria* available in American herbaria. The problem of the North American native canes has been presented in this preliminary manner for several reasons. In the first place, the need for careful study—over a period of years—of the complex throughout its entire distributional range, the extent of this area of distribution, and the infrequent flowering periods of many populations, makes the problem of delimitation of unit-entities in this segment of *Arundinaria* more than a one-man job. Secondly, it is my belief that the herbarium specimens now on file in our museums are not adequate for the delimitation of entities within the genus. At such time as the biology of the group is more thoroughly understood as the result of detailed and extensive field studies, the specimens at present available—together with those which will be collected in the course of future studies—may be utilized in developing the exact distributional patterns of this segment of the genus.[19] And, lastly, since no definite application of names can be made at the present time—the solution of the nomenclatural phase of the problem outlined in this paper, therefore, being scarcely a prospect of the immediate future—it did not seem advisable at present to examine more material than that available in the herbarium of the New York Botanical Garden.[20]

CONCLUSIONS

In current manual treatments of the North American canes (*Arundinaria*) two species are generally recognized. The differentiation between these species has been made on the relative height of the plants and the manner in which the inflorescence is borne. Since there is evidence in the literature

considered as only a growth-form modification of the upland cane. As Dr. Camp has pointed out in our personal discussion of this matter, the epithet *pumila* certainly would be applicable to much of the upland *mississippi-type* material which, on the basis of available evidence, is conspecific with the *mississippi-type* material of the certainly moister and more fertile lowland habitats.

[19] Despite the irregular flowering periods of certain populations of cane, flowering and fruiting material should be obtained whenever possible. In future collections of sterile material it is suggested that collectors make an attempt to obtain from a single plant specimens from both the current season's growth and the canes of preceding years; it also seems advisable that specimens be taken from at least several plants in a single locality in order to determine the degree of variability in each particular area. Moreover, because of the known variability of the group on the Atlantic Coastal Plain and the eastern segment of the Gulf Coastal Plain, mass collections should be made whenever possible in these regions.

[20] The only exceptions to this statement have been my examination of a fragment of a specimen (*Plymale s. n.*) from the only locality in West Virginia in which *Arundinaria* has been collected, and of fragments of two specimens (*Wells s. n.* and *Buell s. n.*) from North Carolina. These fragments, obtained through the courtesy of Dr. E. L. Core, of the University of West Virginia Botany Dept., and Dr. B. W. Wells, of the North Carolina State College Botany Dept., are now deposited in the herbarium of the New York Botanical Garden.

that a single plant may produce both types of flowering culms, the conclusion has been reached by some workers that only one species is present in North America.

A preliminary examination of species available to me indicates that two types of spikelets, differing in several well-defined characters, are present in the North American cane populations. Since the type specimens necessary to the solution of the nomenclatural phase of this problem are not at present available for study, these two entities have been designated the *atlantic-type* (this one being best developed on the Atlantic Coastal Plain) and the *mississippi-type* (this being the only type apparently present in the drainage basin of the Mississippi River). Since the characters of the spikelets appear to be of fundamental value in the classification of the Gramineae, and since both growth-forms are associated with each of the spikelet types, it seems evident that the habital characteristics used in most former treatments of the group are not to be considered as specifically diagnostic. There is also evidence that certain characters of the leaf sheaths are correlated with the spikelet types. On the basis of these leaf sheath characters, the *atlantic-type* seems to have affinities with the South American members of the group, while the *mississippi-type* seems more closely related to certain of the Asiatic members of the genus.

Despite the fact that intermediates have apparently been produced in certain areas where both the *atlantic-* and the *mississippi-types* occur, it is maintained in this paper that two specific entities are present in the North American populations of *Arundinaria*. These may be distinguished by characters of the spikelets and leaf sheaths, but not by the habital characters generally used in the available treatments of the genus.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 3, pp. 310–324 MAY, 1943

WHAT IS THE TRINOMIAL TYPICUS?—I

LEON CROIZAT

In a recent paper (Rhodora **44**: 157. 1942), Fosberg reveals that a proposal is being circulated to have the Botanical Congress rule out in due course the use of the epithets *typicus, genuinus, verus, veridicus*, and the like. Under this proposal the place of these classic epithets should be taken by the epithet in the binomial. Accordingly, it should be illegitimate or unorthodox to publish *Planta una* var. *typica*, the correct form being solely *P. una* var. *una*.

Such a proposal is not new. One fundamentally like it was advanced by Bolle five years ago (Notizbl. Bot. Gart. Berlin **13**: 524. 1937), and three years ago Fosberg proposed likewise to amend Art. 30 of the current Rules (Am. Jour. Bot. **26**: 229. 1939) which is supposed to be responsible for nomenclatural difficulties when *typicus* and its equivalents are being used.

The recurrent nature of these proposals indicates that the Rules now in vigor leave something to be desired and that changes are necessary. My purpose in writing this article is naturally twofold. I intend to analyze the proposal to which Fosberg alludes and that of Bolle in order to determine whether the measures sponsored therein are pertinent and efficacious. This done, I will briefly state what I believe to be the true nature and function of the trinomial *typicus*. So approached in a spirit of exhaustive discussion the subject at hand will yield not only practical and theoretical considerations but a concrete platform for further competent discussion.

Anyone who intends to modify existing rules, be these rules concerned with the sale of milk in the market of Gopher Junction or with the proper use of taxonomic names in the halls of a botanical institution, should have a clear understanding of three requirements. These requirements are: (1) The proposed amendment must be consistent with the rules that already exist. This means that the amendment must consider what rules say and avoid conflicting with their broader aspects. More definitely: intended changes must be neatly and properly grafted on existing regulations; if conflicts arise between the old and new rules, these conflicts must be smoothed out, either by suitably modifying the proposal itself or by altering the rules that are. Loose ends, contradictions, obscurities are abhorrent to a wise reformer. (2) In no case shall the remedy be worse than the evil which it intends to cure. Heavy drinking is an unmitigated curse but enforced prohibition is just as bad, perhaps worse. A would-be reformer must keep in mind that any rule is bound to be imperfect and carefully weigh the consequences of the changes he sponsors, lest these changes open the door to consequences

even less desirable than the existing inconveniences. (3) The proposed remedies must be applied where they do the most good in the most direct manner. It is useless to deal in generalities and pious wishes without stating the manner of their application to specific cases.

These three principles are not controversial because they speak the voice of common sense. A competent horticulturist does not graft a scion two inches thick on a stock an inch wide; a seamstress does not mend a torn spot in a black dress with coarse white thread; a physician does not leave a potion behind without telling the patient how to take it and when. I restate these principles for reasons that will later be apparent to the reader. Whenever a subject is involved which is controversial and obscure, *it is essential to return to fundamentals*, redefining the major premises of the discussion, informing those who seek the light or need it. To build truly we need solid foundations, readable blue-prints, and precise formulae.

In the copy in my hands, the proposal to which Fosberg alludes reads in part as follows:

"Proposal II. Article 30 a. *Each subspecific group, of whatever rank, which includes the type of the species, shall be designated by the valid specific epithet of the species. For nomenclatural purposes this epithet, when used for a subspecific group, has no authority and no citation and can not be transferred, except as the species to which it is subordinated may be transferred. Each subspecific group which includes the type of the next higher subspecific group but which excludes the type of a species shall be designated by the valid subspecific epithet of the next higher group.*"

This proposal is not likely to appeal to the majority of its readers on the ground that it is worded in highly technical language. This, however, is not in itself a blemish, for it is patent that to deal with technical subjects technical language must be used. It is too much to hope that everything can always be written in colloquial sentences. Obviously, the burden of making technical language understandable, and of understanding it, rests evenly upon the shoulder of the writer and of the reader. If both the parties to the transaction prove incompetent or unwilling, nothing will ever be achieved. It is strange that many who object strenuously against technical language in the Rules of Nomenclature prove to be good bridge players, having at their fingertips a vocabulary staggering to the uninitiated in the game.

The proposal just stated consists of four main parts which must be discussed in detail, as follows:

(1) "*Each subspecific group, of whatever rank, which includes the type of the species, shall be designated by the valid specific epithet of the species. . .*"

Article 2 of the current Rules of Nomenclature (Amsterdam, 1935) states: "The object of the rules (Art. 19–74) is to put the nomenclature of

the past into order and to provide for that of the future. They are always retroactive: names or forms of nomenclature contrary to a rule (*illegitimate names or forms*) cannot be maintained." This declaration is imperfectly worded, of course, to the extent that it refers to the Articles as "rules," a term which we commonly use in a looser and broader sense. However, it is perfectly clear that, (a) The Articles are always retroactive; (b) Forms and names contrary to an Article cannot be maintained.

This being the case, the proposal advanced by "Art. 30 a" in the clean-cut words quoted above has for its immediate effect to render illegitimate any of the typic trinomials published after 1753 which does not repeat the specific epithet. I believe that this is not the intention of the proponents of "Art. 30 a," but good intentions are meaningless in a world in which only facts count. Either Art. 2 goes as it reads or "Art. 30 a," for there is war between them. My interest in discussing this proposal will be clear to the reader who is told that about one thousand trinomials using *typicus* or *genuinus* instead of the specific epithet repeated are contained in Volume 15 of De Candolle's *Prodromus* (2) which I consult every day. If "Art 30 a" is approved and written into the Rules, all these trinomials are turned into scrap, scrap of a kind which cannot be used otherwise than as synonymy. It stands to reason that "Art. 30 a" runs afoul also of Art. 4 in the current Rules which reads: "The essential points in nomenclature are: (1) to aim at fixity of names; (2) to avoid or to reject the use of forms and names which may cause error or ambiguity or throw science into confusion. Next in importance is the avoidance of all useless creation of names." It is manifest that "Art. 30 a," if approved, will upset the trinomials now in use, throw science into confusion and foster the creation of thousands of new trinomials to replace those which this "Article" would slaughter. Having pointed out these results of "Art. 30 a" in private conversations, I have been told in return that the existing trinomials using *typicus*, *genuinus* and the like should be "quietly ignored." No objection could be raised against their being ignored, quietly or otherwise, if the authors of this "Article" would only state *how* it is possible to elude the precise disposition of Art. 2 and Art. 4. This, "Art. 30 a" does not say, which is a capital omission.

(2) ". . . *For nomenclatural purposes this epithet, when used for a subspecific group has no authority and no citation.* . . ."

The implications of these seventeen words are staggering, for they contain an entirely novel and revolutionary concept of authority and citation, a concept which is unenforceable on account of conflict with rock-bottom realities. Article 15 in the current Rules states: "The purpose of giving a name to a taxonomic group is not to indicate the characters or the history of the group, but to supply a means of referring to it." Article 46 in the same Rules reads: "For the indication of the name (unitary, binary, or ternary) of a group to be accurate and complete, and in order that the date

may be readily verified, it is necessary to cite the author who first published the name in question." This is plain speaking and common sense. A taxonomic name is a label, no more, no less. If this were not so, names untrue to the characters or to the history of the group naturally ought to be changed. There would be no end to such changes, of course, because every age understands characters and histories in a different light. It is patent, moreover, that the Rules wish to have this label complete, that is, filled with the data making it possible to ascertain without doubt and delay its author and origin. Synonymies were in use long before Linnaeus, and even the oldest among them are careful to state the authorities of the names, this statement being an essential requirement in any citation. Nor is this all: it is only by reference to citations and authorships that priority can be determined.

The same weakness reappears in the statement just quoted from "Art. 30 a" which is manifest in its opening declaration. This weakness consists in the neglect of what the existing Rules say, and in the failure to indicate *how* the proposed reform is to work. Taking "Art. 30 a" at its word, I might not write down on paper such citations as: *Manihot gracilis* Pohl var. *genuina* Muell.-Arg. in DC. Prodr. **15**(2): 1065. 1866; or: *Mallotus oreophilus* α *ochraceo-albidus* Muell.-Arg. in op. cit., 964; but the fact that I could not legitimately write these data would certainly not free me from the duty of knowing precisely where and by whom these trinomials have been published. In cases involving doubt or possible controversy should I write such copy as this: "*Manihot gracilis* Pohl var. —I am forbidden by Art. 30 a (now happily in vigor) to use the original trinomial *genuina* of (authorship cannot be given). I propose, consequently, in obedience to said Article a new variety *gracilis*. If somebody is to cite this variety, let him understand that Art. 30 a forbids him to reveal that I am the author of this name, and that the page and work in which I write this cannot be referred to"? Or shall I write this: "*Manihot Toledii* var. *Toledii* . . .. If the reader wishes to know whether I am right in spelling *Toledii* instead of *Toledi*, will he please look . (authority and citation not to be given under Art. 30 a)"?

What do the proponents and authors of "Art. 30 a" mean when they speak of "*nomenclatural purposes*"? What does it mean that "*A subspecific group has no authority and no citation*"? How is an author to avoid "*authority and citation*" when he uses a taxonomic name, since such a name has definitely been published somewhere by somebody? Even tolerably precise and sound generalities are void of sense when the means are not given to work them against concrete cases; how are we, then, to use vague and unsound generalities?

(3) "*. . . For nomenclatural purposes this epithet . . . can not be transferred, except as the species to which it is subordinate may be transferred. . . .*"

A statement similar to the one quoted is contained in the current Art. 18, this Article being a peculiar compromise between different concepts of type. Article 18 reads: "A nomenclatural type is that constituent element of a group to which the name of the group is permanently attached, whether as an accepted name or as a synonym." It is true that Art. 18 declares that the nomenclatural type of a species is a specimen, description, or figure, but it is none the less true that Art. 18 hardly knows its mind. Witness the *Note* which is an integral part of this Article and says: "The nomenclatural type is not necessarily the most typical or representative element of a group; it is merely that element with which the name of the group is permanently associated." If, as Art. 18 declares, a specimen is indeed the nomenclatural type of a species, the *Note* in question is straight nonsense. A specimen *certainly* is the "most typical or representative element" of a species which is known from a single collection. To make the point clear: how can *Rose 18658* fail to be the "most typical or representative element" of *Trichocereus peruvianus*, when *T. peruvianus* solely rests upon *Rose 18658?* As a matter of fact, Art. 18 refers in its *Note* to a nomenclatural type which is certainly not a specimen, thus belying its own definition. This Art. 18 does because it tries to effect an unsuitable compromise between different concepts of type, confusing as one, (a) a type-circumscription; (b) a type-specimen; (c) a biological type. The *Note* in Art. 18 states in reality that the type subdivision (type-trinomial or type-binomial, type-genus or type-family) is not necessarily the most typical or representative element of the group (species, genus, family, or order) in the biological sense. It is merely that element to which the name is permanently attached. To exemplify: *Planta una* var. *typica* is not necessarily the most typical or representative element of the biological complex understood as *P. una*. It is merely the trinomial that cannot be transferred out of *P. una*. Clearly, specimens have nothing to do with this, nor have descriptions and illustrations.

Although illuminating and interesting, the history of Art. 18 cannot now be told because it is not germane to the subject immediately at hand. Suffice it to say that this Article appeases, without effectively compromising, two historic concepts of type, the American revolving around *type-specimens*, and the classic European centering around *type-names*. Readers who may be inclined to doubt the existence of these concepts are referred to a good authority, Greenman (Bull. Torrey Club **67**: 372. 1940), who is qualified to speak by his mature experience with both European and American botanical thought and usage.

Article 18, indirectly and imperfectly, it is true, but none the less effectively takes care of the dictum of "Art. 30 a" when it states that the nomenclatural type and the group for which it stands are "permanently attached." Obviously, the attachment being permanent, the nomenclatural type (for

instance, *Planta una* var. *typica*) and the group for which it stands (*P. una*) cannot be transferred apart, but must be moved together. Article 18, as a matter of the record, goes so far as to specify that the permanency of the attachment endures even if the nomenclatural type and its group are synonyms of other names; which is redundant, as it may not occur to anybody having any smattering of nomenclature to put *P. una* in synonymy and to treat *P. una* var. *typica* as valid or legitimate. It is patent that "Art. 30 a" is not needed, but a redefinition of Art. 18 is much to be desired, purging this Article of the contradictions which make of it a water-logged wreck rather than a trim vessel.

(4) "*Each subspecific group which includes the type of the next higher subspecific group but which excludes the type of the species shall be designated by the valid subspecific epithet of the next higher group.*"

This declaration has moved me to appreciate at long last the wisdom of the saying that the Rules should be let alone to prove themselves for a thousand years. Several months of meditation have not cleared in my understanding the purposes of "Art. 30 a" in respect to the statement just quoted. I am dubious as to my interpretation of it, and only time, long time, will tell whether I have succeeded in piercing the veil of Isis and really approached the sanctum. Naturally, I offer my interpretation of this part of "Art. 30 a" for what it is worth, and shall willingly stand corrected if I have failed to clutch its vitals.

If I read this prose aright, I understand that *Planta quaevis* subsp. *una*, which is not the type-subspecies of the binomial, this being *P. quaevis* subsp. *quaevis* (or *typica*, *genuina*, or the like), can have as its typic variety only *P. quaevis* var. *una*. In other words: the principle would seem to be reaffirmed here that *P. quaevis* shall have as its typic trinomials only subsp. *quaevis*, var. *quaevis*, and forma *quaevis*, whereas *P. quaevis* subsp. *una* shall be followed by such typic trinomials as var. *una* and forma *una*.

If this is the case, "Art. 30 a" displays praiseworthy consistency, its standards in this particular respect being higher than those of Art. 18, which roundly contradicts itself. However, the very same objection rises here that I have invoked before, namely, every trinomial which fails to comply with "Art. 30 a" is made illegitimate. The point does not need to be elucidated and discussed once again. I will emphasize the fact, however, that it is not easy to handle chains of trinomials, and that to make this handling twice as difficult by enforcing unnecessary shibboleths is hardly an evidence of wisdom. The principle that best serves here is, on the contrary, that arbitrary shackles must not be provided to hamper individual freedom in cases that are in themselves hard to manage. Let things stand as they are, so long as it is not absolutely necessary to modify them. Houses of cards are not made steadier by tinkering around the corners in order to have all edges running

true to perpendicular. Such houses look better in theory when they are straightened up, but in practice they fall to the ground. Anybody who handles as his daily fare the trinomials of Briquet, Hackel, Ascherson & Graebner, Mueller Argoviensis, and such past masters in the use of half-tones will not feel kindly disposed toward hands that reach out to make the game harder than it is. To abstain from reforms which are both unnecessary and unwanted is the earmark of a philosopher.

It seems hardly necessary to discuss the "Argument" that bolsters "Art. 30 a." Only two statements in it may be paid cursory attention for the sake of a well rounded analysis. Quoth the "Argument" this much: ". . . *Proposal II does away with the use of such terms as* typica, originalis, *and the like, all of which have occasionally been misinterpreted as indicating the phylogenetic type of the species. . . . Since subspecific groups are not included in the Index Kewensis, this proposal simplifies nomenclatural investigations in taxonomic work and, since authorities are not cited, it obviates cumbersome double citations for many subspecific groups.*"

The fact that *typicus, genuinus* and the like have been occasionally misinterpreted as indicating the phylogenetic type of species, or other things, does not prove that these epithets should be blotted out, granted that it were possible to do so, which it is not. It merely means that those who abuse these trinomials and misunderstand them should be properly instructed by competent teachers, and forever furnished Articles and Recommendation that are well conceived and thoughtfully worded. The fact that a knife cuts one's finger when mishandled does not constitute a valid reason why a turkey should be torn to pieces by hand instead of being neatly carved with good steel. Since the Index Kewensis does not list subspecific epithets, and trinomials are as a rule much harder to trace back than binomials, nothing should be done in principle to disturb them without absolute necessity. The hope that nomenclatural investigations can be simplified by withholding the citations of authorities is most peculiar, for it is only by citing these authorities fully and correctly that nomenclatural investigations can be made simpler. It might facilitate my own task not to cite authorities, but this certainly will make harder the task of my neighbor. Nor is this all: if my neighbor decides to ease his own work by following my lead, it is I who stand at the receiving end. Bibliographical work is as much of a burden to a taxonomist as answering night calls is to a physician, yet each profession must be taken at its face value, putting up with its emoluments and liabilities.

In conclusion: it is certain that "Art. 30 a" is shot through by fallacies so glaring that it should be promptly withdrawn from circulation, its substance being such that it cannot be improved by hopeful manipulations. This "Article" violates in a precise and direct manner Art. 2, Art. 4, Art. 15, and Art. 46 of the Rules now in vigor, a circumstance that its authors ap-

pear to have overlooked altogether; it advances a new theory of citation which is of impossible application; it lays hands upon an Article (Art. 30) which, as will be seen, is not at all concerned with the reforms intended; it wanders aimlessly to introduce a change in the Rules which can easily be effected by a slight addition to Art. 55, which soon will be apparent; to achieve a single worth-while purpose, providing for the difficulties arising when *typicus, genuinus,* and the like are transferred, it merely repeats a dictum which is already poorly stated in Art. 18. In brief, if the simile may be forgiven, this "Article" wrecks a house in order to dig out a penny from under a table. That this "Article" is withdrawn without causing further doubts and confusion is a legitimate hope, this hope also justifying the passing in silence of all other proposals that go with "Art. 30 a," and are not better grounded than it.

The proposal of Bolle that affects the typic trinomial, although based on a misapprehension, cannot be said to be objectionable in its essence. Bolle points out in substance that when *Acomastylis elata* var. *typica* is transferred to *A. Peckii,* the resulting new combination must be *A. Peckii* var. *typica.* This combination, Bolle further points out, is erroneous because the typic variety of *A. elata* is not the typic variety of *A. Peckii.* Moved by this knowledge, Bolle asks that a Recommendation, *not an Article,* be written into the Rules to discourage the use of *typicus, genuinus,* and the like, urging on the contrary that the specific epithet be repeated. Accordingly, if *A. elata* var. *elata* is to go under *A. Peckii* a new combination results, *A. Peckii* var. *elata,* which is satisfactory.

The misapprehension in Bolle's thought arises from the fact that a Recommendation is neither retroactive nor mandatory. Accordingly, Bolle's proposed Recommendation is powerless to eliminate the inconveniences arising from the transfer of *typicus* and its equivalents, *genuinus, verus,* and the like. This Recommendation is a broken reed, and falls short of what Bolle hopes to secure from it. To elucidate the point at issue, let us suppose that a taxonomist is faced in 1952 by the problem of transferring *Manihot gracilis* var. *genuina* Muell.-Arg. (1866) to *M. tenuifolia.* This taxonomist cannot reject the variety, for it is legitimate and must, somehow, transfer it in a manner other than by moving *genuina* under *M. tenuifolia.* If Bolle had his wish come true, this taxonomist turning to the Rules to learn how to act would find therein a Recommendation urging that after 1950, let us say, no variety *genuina* should be published. Naturally, this much would not help the inquiring taxonomist in the slightest, for his interest would be to learn how to act at the moment, transferring a trinomial *genuina* legitimately published in 1866.

It is patent, consequently, that neither by forbidding the use of *typicus, genuinus,* and the like *in an Article* nor by discouraging it *in a Recommen-*

dation can the problem be solved which disturbs the authors of "Art. 30 a" and the sponsors of Bolle's "Recommendation." The solution, obviously, must be sought elsewhere. To find this solution is most easy. There is an Article in the Rules now in vigor which orders that in transferring a subdivision of a species to another species the earlier legitimate epithet must be maintained. *This is the Article*[1] *to be modified because it is the one immediately concerned with the matter.*

Article 55 reads: "When a variety or other subdivison of a species is transferred, without change of rank, to another genus or species (or placed under another generic or specific name for the same genus or species) the original subdivisional epithet must be retained or (if it has not been retained) must be re-established, unless one of the following obstacles exists: (1) that the resulting ternary combination has been previously and validly published for a subdivision based on a different type, even if that subdivision is of a different rank; (2) that there is an earlier validly published subdivisional epithet available." Shorn of technical trappings, this text means that the original specific epithet must be shifted without being changed, unless the shift creates a later homonym or a synonym. Naturally, this text orders that the trinomial *typicus*, too, be transferred, for it speaks of *all* subdivisions, without making exception for *typicus* and its kindred.

To remedy this situation, therefore, a clause must be added to Art. 55 which exempts the trinomial *typicus, genuinus,* and the like from transfers, and asks that the first meaningful epithet of higher rank be moved instead. This can be done by the following addition to Article 55: ". . . (3) that a trinomial epithet *typicus, genuinus, verus, veridicus,* or the like (cf. Rec. xviii and Rec. xxxv) is to be transferred. In this case the epithet of the name next above in rank other than *typicus, genuinus,* etc., shall be transferred . . . Examples: . . . *Acomastylis elata* var. *typica* when transferred to *A. Peckii* becomes *A. Peckii* var. *elata* not *A. Peckii* var. *typica.*—*Planta quaevis* var. *typica* f. *genuina* put under *Arbor qualis* becomes *A. qualis* var. *quaevis* f. *quaevis.*—*Frutex unicus* subsp. *quilibet* var. *originarius* moved to *Caulis magnus* is turned into *C. magnus* subsp. *quilibet* var. *quilibet.*"

This solution is liable to modifications and changes as a matter of course, if concrete evidence shows that it must be altered in detail or enlarged to take care of special cases. To discuss in full is bound to be constructive, and I shall welcome the opportunity to be shown where and how I might have

[1] Article 55 will have to be modified at any event, for it fails to foresee the difficulties which arise when the trinomial *typicus, genuinus,* and the like are transferred in obedience to its present dicta. However, the proper place to deal with anything pertaining to types is in Section 2 of the Rules, which deals with "The type method." I refrain from discussing this Section in full here, because such a discussion would not be wholly germane to the subject under present consideration.

erred in drawing it up in its present form. It is conceivable that some reader knows of examples that have escaped my notice and bear directly upon the text here outlined. However, it may be stated that this solution, regardless of details, is simple and forcible for two reasons: (1) It directly acts upon the Article involved and does not ramble so as to lay hands upon Articles that are unrelated with the subject; (2) It takes due account of the fact that *A. elata* and *A. elata* var. *typica* are both typified by the very same specimen. Since, in the last analysis, it is this specimen which must become the type-specimen of the new variety under *A. Peckii*, it is irrelevant that the name given to this specimen is drawn from the binomial rather than from the trinomial. To elucidate: *Wallich, Sirmore & Kemaon* is the type-specimen of both *A. elata* and *A. elata* var. *typica*, while *Peck in herb. Banks.* is the type-specimen of *A. Peckii*. When *A. elata* is brought as a variety under *A. Peckii*, the new combination expressed on the basis of the specimens can be stated as follows: *Peck in herb. Banks.* has for its variety *Wallich, Sirmore & Kemaon*. It stands to reason that since the latter specimen typifies both *A. elata* and *A. elata* var. *typica*, we may use *elata* rather than *typica* as a matter of free choice, without doing violence to the inherent truth of the transfer. Naturally, the new combination *A. Peckii* var. *elata* is satisfactory. The fact that the authors of "Art. 30 a" and Bolle failed to discover this egg of Columbus seems to be due to lack of familiarity with the Rules, and with a less than perfect understanding of the nature of the trinomial *typicus*.

It is probable that some taxonomists will choose to believe that a modification of Art. 55 requires a change also in Art. 58, which—in their understanding—is supposed to order that an older valid name is transferred when the rank is changed. These taxonomists take it for granted, for instance, that when *Planta una* var. *lacta* becomes a species, the new name must be *P. lacta* comb. nov. If this interpretation be true, Art. 58 should be modified together with Art. 55 to provide for the special case involved by the transfer of *typicus* and its equivalents. It is my definite understanding that Art. 58 does not require a modification to take care of *typicus* and like epithets. However, a not irrelevant segment of botanical opinion implicitly holds to the opposite view. Naturally, I am bound to state my reasons in order that those who believe I am in error may expose the fallacies of which I am guilty, if possible, showing how Art. 58 must be modified in regard to the typic trinomial.

In the Code of Paris of 1867, Art. 58 stated: "Lorsqu' une tribu devient famille, qu'un sousgenre ou une section devient genre, qu'une subdivision d'espèce devient espèce, ou que des changements ont lieu dans le sens inverse, les noms anciens des groupes subsistent, pourvu qu'il n'en résulte pas deux genres du même nom dans le règne végétal, deux subdivisions de genre ou deux espèces du même nom dans le même genre, ou deux subdivisions du

même nom dans la même espèce.'' (When a tribe becomes a family, a subgenus or a section becomes a genus, a subdivision of a species becomes a species or the reverse of these changes take place, the old names are maintained so long as the result of this maintenance does not call for a later homonym of generic, specific or subspecific rank.) This text is definite to the effect that, for instance, *Magnolia virginiana* var. *foetida* L. (1753) must become *M. foetida* (L.) Sarg. (1889) as a species, the older epithet (*foetida*) persisting in the new combination. In his ''Commentaires,'' Alphonse De Candolle, the author of this Article, states as a matter of fact (Lois Nom. Bot. 61. 1867): ''Les dispositions de ces articles (*57, 58*) paraîtront nouvelles à plusieurs botanistes, du moins en ce qui concerne les modifications d'espèce. Elles sont cependant utiles pour empêcher la multiplication des noms et aider la mémoire en cas de mutation de place ou de rang. Plusieurs auteurs exacts les observent depuis longtemps.'' (The rulings in these Articles (*57 and 58*) will strike some botanists as novel, at least so far as they concern the remodeling of species. These rulings will serve, however, as checks upon the needless publication of new names and will provide useful reminders when names change their position and rank. These rulings are already being followed by several critical botanists.)

No one would think of using today the Paris Code of 1867 for the simple reason that, despite its fundamental nature and its inherent perfection, in it weaknesses and blemishes were revealed. For instance: Art. 56 of this Code has been dropped. It stated: ''Lorsqu'on divise une espèce en deux ou plusieurs espèces, si l'une des formes a été plus anciennement distinguée, le nom lui est conservé.'' (When a species is remodeled into two, the binomial is maintained for that part which has [trinomially] been designated first.) This dictum was hardly sound, for it could lead to the acceptance of the first published trinomial as typic of the binomial; accordingly, Boissier's *Euphorbia Nagleri* β *baliensis* would have been typified by the trinomial *baliensis* against Boissier's own intentions in designating this variety with the letter β instead of α, the latter being accepted according to good usage as the connotation of the typic variety. Clearly, the type-variety of *E. Nagleri* is an as yet unpublished trinomial *typicus* or *Nagleri*, based upon *Nagler in herb. Berol.*, not upon *Zollinger 2975*, which is the type-specimen of β *baliensis*.

Article 58 of the Paris Code has been maintained under the same number in the International Rules of Amsterdam (1935). In the English text, this Article reads: ''When a tribe becomes a family, when a subgenus or section becomes a genus, when a subdivision of a species becomes a species, or when the reverse of these changes take place, and in general when a group changes its rank, the earliest legitimate name or epithet given to the group in its new

rank is valid, unless that name or the resulting association or combination is a later homonym (see Art. 60, 61)."

This Article has been proposed for modifications and it is notoriously ambiguous. Its ambiguity, however, is not of the fundamental nature which taints Art. 18, but is due to careless editing, a blemish apparent at several points in the Rules. This Article clearly consists of two parts, namely: (1) "When a tribe becomes a family, when a subgenus or section becomes a genus, when a subdivision of a species becomes a species, or when the reverse of these changes take place, and in general when a group changes its rank, the earliest legitimate name or epithet given to the group in its new rank is valid, . . . Examples: The section *Campanopsis* R. Br. (*Prodr. Fl. Nov. Holl.* 561: 1810) of the genus *Campanula* was first raised to generic rank by Schrader, and as a genus must be called *Wahlenbergia* Schrad. (*Cat. Hort. Goett.:* 1814), not *Campanopsis* (R. Br.) O. Kuntze (Rev. Gen. II, 378: 1891).—The var. *foetida* L. (*Sp. Pl.* ed. 1. 536: 1753) of *Magnolia virginiana*, when raised to specific rank, must be called *Magnolia grandiflora* L. (*Syst. Nat.* ed. 10, 1082: 1759), not *Magnolia foetida* (L.) Sarg. (in *Gard. and For.* II, 615: 1889)—*Lythrum intermedium* Ledeb. (*Ind. Hort. Dorp.:* 1822), when treated as a variety of *Lythrum Salicaria* L., must be called *L. Salicaria* var. *glabrum* Ledeb. (*Fl. Ross.* II, 127: 1844), not *L. Salicaria* var. *intermedium* (Ledeb.) Koehne (in Engl. *Bot. Jahrb.* I, 327: 1881). In all these cases the name or epithet given to the group in its original rank is replaced by the first legitimate name or epithet given to it in its new rank."

There is not the slightest possibility of reading this text and its examples to mean that the epithet or name given to a group in a rank must be maintained in another rank. *Campanopsis*, *foetida*, *intermedium* are the *oldest names* given to a certain entity, yet these names fall against *Wahlenbergia*, *grandiflora* and *glabrum* which are *later names* given to the very same entity in a different rank, genus instead of section, species instead of variety, variety instead of species. Article 58 of the current Rules, consequently, unequivocally contradicts Art. 58 of the Paris Code of 1867; one says white, the other black.

Article 58 of the current Rules, however, continues after the text just quoted as follows, (2) ". . . , unless that name or the resulting association or combination is a later homonym (see Art. 60, 61)." This ending is absolutely meaningless in view of the text that precedes it. The text that precedes it—as it has been seen—flatly rules out new combinations effected to retain the older names. Why, then, anything at all should be said here about new combinations being possible later homonyms? It is understood that if *Wahlenbergia, Magnolia grandiflora,* and *Lythrum Salicaria* var. *glabrum* are later homonyms they must go, for this happens to every name in taxonomy which is a later homonym, inside and outside the purview of Art. 58.

As I have said, this meaningless and confusing addition to Art. 58 is the result of careless editing. While the *substance* of Art. 58 of the Paris Code, 1867, has been radically altered in the new Art. 58, the one saying black where the other said white, the new Art. 58 has been worded in a *form* that befits,—to a very small extent, it is true,—the old Article of the same number. Careless editing of the kind, leading to endless misinterpretations and futile arguments, is in evidence here and there in the Rules and should be corrected. What Art. 58 of the current Rules *actually* states is very plain, for the meaning of this Article is to be read in five lines of its text and in all its examples, the whole ringing as clear and as true as a bell. The obnoxious and misleading rump of this Article is one printed line that hangs in the air. *This line must go,* the sooner the better. Naturally, I do not believe that the modification I propose to introduce in Art. 55 has anything to do with Art. 58, for the two Articles are not at all germane. One (Art. 55) regulates transfers involving the *same rank* (subspecies to subspecies, variety to variety, form to form and the like); the other (Art. 58) concerns transfers effected in a *different rank* (section to genus, species to variety, variety to species), which is a very different matter. To overstress a line of print which hangs from the window sill of Art. 58 without rhyme or reason, this in order to have two basically sound Articles become confused in their purposes and ultimate concepts, is not commendable. A correction, not an "interpretation" is here in order.

It is not clear why the reformers of the trinomial *typicus* tilt with Art. 30, and attempt to plaster it with their manifestoes when this Article has basically nothing to do with *typicus*. It is peculiar, none the less, that this same Article should be widely misunderstood in other directions.

Article 30 reads as follows: "Two subdivisions of the same species, even if they are of different rank, cannot bear the same subdivisional epithet, unless they are based on the same type. If the earlier subdivisional name (ternary combination) was validly published, the later one is illegitimate and must be rejected." Some authors believe that this Article establishes the principle that all trinomials have the same rank, that is, for purposes of priority a subspecies is tantamount to a variety or a form, building on this belief strange constructions of their own making. Other authors, like the sponsors of "Art. 30 a" see in this text obscure meanings that involve the typic trinomial.

The truth is plainly otherwise and to prove it is easy indeed. Let us suppose that *Planta una* has a subspecies *rubra* (1900), and that *Arbor quaevis* has a variety *rubra* (1930), too. Let us next suppose that the var. *rubra* of *A. quaevis* is transferred under *P. una*. Effected in the usual manner this transfer gives: *Planta una* subsp. *rubra* var. *rubra*. This, Art. 30 states, can-

not be done. The reason is simple: anyone who reads this citation understands automatically that the variety is typic of the subspecies because both the subspecies and the variety have the same epithet, *rubra*. This would certainly not be true if subsp. *rubra*, for instance, were a hairy plant and var. *rubra* a glabrous one, the type-specimens of the two being different. To prevent such a confusion from arising, Art. 30 wisely arranges that var. *rubra*, which is later in point of publication, must lose its name when transferred under *P. una* and become, for instance, var. *nigra*, for the citation then reads: *P. una* subsp. *rubra* var. *nigra*, which lends itself to no ambiguity. Naturally, if subsp. *rubra* had been published later than var. *rubra*, it should be the subspecies rather than the variety to change its name. Lastly, Art. 30 allows for the case in which var. *rubra* happens to be the type-subdivision of subsp. *rubra*, making it possible to retain both without alteration.

This interpretation of Art. 30 might be challenged as overdrawn on the strength of one of the examples introduced under the Article which reads: "The following is incorrect: *Erysimum hieraciifolium* subsp. *strictum* var. *longisiliquum* and *E. hieraciifolium* subsp. *pannonicum* var. *longisiliquum*—a form of nomenclature which allows two varieties bearing the same name in the same species," nothing being stated about the transfers which I have chosen to illustrate my interpretation of the Article. This challenge deserves an answer, for it is based on the appearance of fact and works to the point.

Clearly, there should be no reason to forbid the use of var. *longisiliquum* under different subspecies of the same binomial unless for the purpose of avoiding a possible confusion between the two homonymous trinomials in question. Aside from thoughtlessness in reading the citations, which is not a matter for the Rules to take under consideration unless in the very broadest sense, such a confusion might arise in two manners: (1) By the use of an abbreviated citation such as is authorized by Art. 28. This use need not be indulged in, for Art. 28 merely states: "It is permissible to reduce more complicated names to ternary combinations. Examples— . . . *Saxifraga Aïzoon* subforma *surculosa* Engl. et Irmsch. is permissible for *Saxifraga Aïzoon* var. *typica* subvar. *brevifolia* forma *multicaulis* subforma *surculosa* Engl. et Irmsch." Naturally, no critical taxonomist will take advantage of a concession made in the Rules if this leads to ambiguity, because ambiguity is forbidden (see Art. 4); (2) By a transfer of trinomials from one species to another. Here the danger of confusion is definite, for the older epithet is transferred in principle (Art. 55) if the rank remains the same. If Art. 30 were not in the Rules, Art. 55 ought to contain its basic provisions, nevertheless. Naturally, to illustrate Art. 30 I have deliberately chosen an example that illustrates *the necessity* of this Article rather than one which shows only *its desirability*. This, I believe, is consistent with general criteria of sound

interpretation. It is obvious that Art. 30 was written by a competent student of nomenclature basically to take care of a special case. So special is this case, as a matter of fact, that Art. 30 is usually not understood, this serving as a curious illustration of the danger of feeding the best of fare to guests accustomed to coarse stew. Article 30, naturally, has nothing to do with the generalities underlying the typic trinomial and even less can it be construed to mean that all trinomials have the same rank. It will be seen that Art. 55 (1), too, vetoes the transfer of a trinomial, *regardless of its rank,* if this trinomial should prove to be a homonym. It is unfortunate that Art. 55 (1) is improperly worded, in failing to specify that it refers to trinomials *under the same species.* This, however, is rectified by the general principle contained in Art. 30.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)
(See also under General Botany: **Dodd & Gershoy**)

Allard, H. A. *Lamium amplexicaule* L. forma *clandestinum* (Reichenb.) G. Beck. Va. Jour. Sci. **3**: 125, 126. My 1942 [Mr 1943].

Allard, H. A. Three plants new to West Virginia. Castanea **7**: 114–118. D 1942.

Anderson, E. The seeds of *Tradescantia micrantha*. Ann. Mo. Bot. Gard. **30**: 69. *f. 1.* 22 Mr 1943.

Bailey, L. H. Species Batorum. The genus *Rubus* in North America (north of Mexico). V. Section 6. Flagellares. The dewberries. Gentes Herb. **5**: 231–422. *f. 98–191.* 15 Mr 1943.

Barneby, R. C. Miscellaneous diagnoses. Leafl. West. Bot. **3**: 193–199. F 1943.

Bartram, E. B. Mosses collected by Hawaiian Bog Survey of 1938. Bishop Mus. Occ. Pap. **16**: 321–336. *f. 1–3.* 15 Ap 1942.

Bartram, E. B. Mosses of Papua, New Guinea. Farlowia **1**: 41–47. *f. 1–16.* Ja 1943.

Boehner, P. The Hepaticae of Catteraugus County. Sci. Stud. St. Bonaventure Coll. **11**[8]: 11–15. Mr 1943.

Boivin, B. The "Coûdres" of the "Ysle en Couldres." Rhodora **45**: 29–31. 13 F 1943.

Chen, L. A revision of the genus *Sabia* Colebrooke. Sargentia **3**: 1–75. *f. 1–9.* 30 Ja 1943.

Cory, V. L. The perennial *Helenium* of the Edwards Plateau of Texas. Rhodora **45**: 109–111. 17 Mr 1943.

Cozzo, D. El arbolado de las calles de la ciudad de Buenos Aires. Rev. Arg. Agron. **9**: 354–376. D 1942.

Croizat, L. *Thalictrum ametrum* Greene: an interesting nomenclatural case. Madroño **7**: 1–4. 28 Ja 1943.

Crevetto, R. M. Las gramineas argentinas del género *Echinochloa*. Rev. Arg. Agron. **9**: 310–342. *f. 1–8.* D 1942.

Cuatrecasas, J. Notas a la flora de Colombia, V. Rev. Acad. Colombiana **5**[17]: 16–39. *pl. 1–3* + *f. 1–22.* Ja–Je 1942.

Dixon, H. N. Alpine mosses from New Guinea. Farlowia **1**: 25–40. Ja 1943.

Drouet, F. New species of Oscillatoriaceae. Am. Midl. Nat. **29**: 51–54. Ja 1943 [6 Mr 1943].

Dunkle, M. B. Contributions from the Los Angeles Museum—Channel Islands Biological Survey No. 27. Flora of the Channel Islands National Monument. Bull. S. Cal. Acad. **41**: 125–137. *pl. 26, 27.* S–D 1942. [31 Ja 1943].

Eastwood, A. *Gilia salticola* Eastw. nom. nov. Leafl. West. Bot. **3**: 199. F 1943.

Eastwood, A. New western lupines. Leafl. West. Bot. **3**: 202–204. F 1943.

Egler, F. E. The Seashore State Park, a part of Cape Henry, Virginia. Rhodora **45**: 105–107. 17 Mr 1943.

Erickson, R. O. Population size and geographical distribution of *Clematis Fremontii* var. *Riehlii.* Ann. Mo. Bot. Gard. **30**: 63–68. *f. 1–4.* 22 Mr 1943.

Erickson, R. O. Taxonomy of *Clematis* section *Viorna.* Ann. Mo. Bot. Bard. **30**: 1–62. *pl. 1.* 22 Mr 1943.

Farwell, O. A. *Cornus*, a reply. Torreya **42**: 130. 29 Ja [13 F] 1943.

Fernald, M. L. *Scirpus Longii* in North Carolina. Rhodora **45**: 55, 56. 13 F 1943.

Fernald, M. L. Two later homonyms. Rhodora **45**: 111, 112. 17 Mr 1943.

Frye, W. M. Notes on the flora of the South Branch valley. Castanea **7**: 118–122. D 1942.

Gilbert, W. J. Studies on Philippine Chlorophyceae. I. The Dasycladaceae. Pap. Mich. Acad. **28**^{1} (1942): 15–36. *f. 1–3.* F 1943.

Gilly, C. L. Studies in the Sapotaceae, II. The sapodilla-nispero complex. Trop. Woods 73: 1–22. 1 Mr 1943.

Gleason, H. A. & Pierce, J. H. Two new species of *Hypericum* from Colombia. Bull. Torrey Club **70**: 174. 1 Mr 1943.

Groh, H. Hackberry in the Ottawa district. Canad. Field Nat. **56**: 130. N–D 1942 [15 F 1943].

Hanes, C. R. Additions to the flora of Michigan. IV. Pap. Mich. Acad. **28**^{1} (1942): 37–40. F 1943.

Harper, R. M. *Croomia* a member of the Appalachian flora. Castanea **7**: 109–113. D 1942.

Herre, A. W. C. T. A few lichens from Indiana. Am. Midl. Nat. **29**: 117–118. Ja 1943 [6 Mr 1943].

Hosaka, E. Y. A new Hawaiian *Panicum* (Gramineae). Bishop Mus. Occ. Pap. **17**: 67–69. *f. 1.* 6 My 1942.

Howell, J. T. Plantae occidentales—III. Leafl. West. Bot. **3**: 205–208. 1943.

Howell, J. T. Studies in *Phacelia*—a revision of species related to *P. pulchella* and *P. rotundifolia.* Am. Midl. Nat. **29**: 1–26. Ja 1943 [6 Mr 1943].

Irenée-Marie, Frère. Étude de la flore desmidiale de la région du Lac St. Jean. Nat. Canad. **69**: 248–259. O–N 1942. 275–282. D 1942.

Jones, G. N. & Jones, F. F. A revision of the perennial species of *Geranium* of the United States and Canada. Rhodora **45**: 32–53. 13 F 1943.

Kearney, T. H. A new cliff-rose from Arizona. Madroño 7: 15–18. 28 Ja 1943.

Lakela, O. Rediscovery of *Caltha natans* in Minnesota. Rhodora **45**: 53–55. 13 F 1943.

Laughlin, E. E. Flora of Barnesville, Ohio. Jour. Gray Mem. Bot. Assoc. **10**: 11–13. Ja 1943.

Ledingham, G. F. & Fraser, W. P. Notes on the Cyperaceae of Saskatchewan. II. *Carex.* Am. Midl. Nat. **29**: 42–50. Ja 1943 [6 Mr 1943].

Leonard, E. C. Four new species of Acanthaceae from Guatemala. Jour. Wash. Acad. **33**: 60–62. 15 Mr 1943.

Lepage, E. Notes sur la flore du Témiscouata. Nat. Canad. **69**: 264–274. D 1942.

Lowe, J. L. *Cladonia alpicola* in New York state. Pap. Mich. Acad. **28**[1] (1942): 63–65. *f. 1.* F 1943.

Mackie, W. W. Origin, dispersal, and variability of the lima bean, *Phaseolus lunatus.* Hilgardia **15:** 1–28. *pl. 1, 2 + f. 1.* Mr 1943.

Magnusson, A. H. Lichens of Nihoa and Necker Islands. Bishop Mus. Occ. Pap. **17:** 25–41. 25 Mr 1942.

Marie-Victorin, Frère, **Rousseau, J. & Cailloux, M.** Le *Cirsium minganense* est-il une bonne espèce? Nat. Canad. **69:** 240–247. *f. 1–4.* O–N 1942.

Marion, L. H. The distribution of *Adenostoma sparsifolium.* Am. Midl. Nat. **29:** 106–116. *pl. 1–4.* Ja 1943 [6 Mr 1943].

Marshall, W. T. *Harrisia Nashii.* Cactus & Succ. Jour. **15:** 3. *f. 2.* Ja 1943.

Martinez, M. Une nueva especie de *Pinus* mexicano. Madroño **7:** 4–8. *pl. 1 + f. 1.* 28 Ja 1943.

Merrill, E. D. & Chen, L. The Chinese and Indo-Chinese species of *Ormosia.* Sargentia 3: 77–117. 30 Ja 1943.

Moldenke, H. N. The flora of the North Appalachian Experimental Watershed and surrounding territory. U S D A Soil Conservation Service, Coshocton, Ohio. 58 mimeographed pages. 21 Ja 1943.

Moldenke, H. N. Noteworthy plant records and nomenclatural notes. Castanea 7: 123–125. D 1942.

Moran, R. A revision of *Dudleya,* subgenus Stylophyllum I. Desert **14:** 190–192. D 1942. II. **15:** 9–14. *illustr.* Ja 1943.

Moscosco, R. M. Catalogus florae Domingensis (catalogo de la flora Dominicana). Parte 1 Spermatophyta. i–xlviii, 1–732p. the author New York. 30 Ja 1943.

Norton, J. B. S. The rose-colored *Polygonum* of Southern Maryland. Castanea 7: 126. D 1942.

Prescott, G. W. & Scott, A. M. The desmid genus *Micrasterias* Agardh in southeastern United States. Pap. Mich. Acad. **28**[1] (1942): 67–82. *pl. 1–6 + f. 1–2.* F 1943.

Proctor, G. Check list of the ferns of Washington County, Ohio. Jour. Gray Mem. Bot. Assoc. **10:** 3, 4. Ja 1943.

Rickett, H. W. *Cornus* again. Torreya **49:** 131. 29 Ja [13 F] 1943.

Rousseau, J. La forme naine du *Plantago juncoides* et autres espèces. Nat. Canad. **69:** 234–239. *f. 1, 2.* O–N 1942.

St. John, H. New Hawaiian species of *Peperomia.* Hawaiian plant studies 10. Occ. Pap. Bishop Mus. **17:** 171–175. *f. 1–2.* 10 F 1943.

Schweinfurth, C. A new *Epidendrum* from Peru. Am. Orchid Soc. Bull. **11:** 360, 361. *pl. 10.* Mr 1943.

Scully, F. Sedges and rushes of Hot Springs National Park and vicinity. Torreya **42:** 129, 130. 29 Ja [13 F] 1943.

Shinners, L. H. A revision of the *Liatris scariosa* complex. Am. Midl. Nat. **29:** 27–41. Ja 1943 [6 Mr 1943].

Soriano, A. Las especies del género *Suaeda* en la Republica Argentina. Rev. Arg. Agron. **9:** 343–353. *f. 1–4.* D 1942.

Stokes, S. G. Further studies in *Eriogonum*—V. Leafl. West. Bot. **3:** 200–202. 1943.

Taylor, W. R. Marine algae from Haiti, collected by H. H. Bartlett in 1941. Pap. Mich. Acad. **28**[1] (1942): 143–163. *pl. 1–4.* F 1943.

Tehon, L. R. Fieldbook of native Illinois shrubs. Ill. Nat. Hist. Surv. Manual 3: 1–307. *6 col. pl. + f. 1–72.* D 1942.

Tseng, Cheng Kwei. Marine algae of Hong Kong. III. The genus *Bostrychia*. Pap. Mich. Acad. **28**[1] (1942): 165–183. *pl. 1–3*. IV. The genus *Laurencia*. 185–208. *pl. 1–4*. F 1943.

Whelden, R. M. Notes on New England algae III. Some interesting algae from Maine. Farlowia **1**: 9–23. *f. 1–18*. Ja 1943.

Wherry, E. T. Guide to eastern ferns. 2nd ed. rev. & enl. Lancaster, Science Press. 1–252. *illustr.* S 1942.

Williams, L. Exploraciones botánicas en le Guayana Venezolana. 1—El medio y bajo caura. Caracas, Servicio botanico, Ministerio de Agricultura y cria. 1–468. *f. 1–53*. 1942.

Williams, L. O. A new *Laelia* from Mexico. Am. Orchid Soc. Bull. **11**: 328, 329. *pl. 9*. F 1943.

Woodson, R. E. & Schery, R. W. Contributions toward a flora of Panama. VII. Miscellaneous collections, chiefly by H. van Wedel, in Bocas del Toro. Ann. Mo. Bot. Gard. **30**: 83–96. *f. 1–2*. 22 Mr 1943.

Yuncker, T. G. Botanizing on Niue Island. Torreya **42**: 121–128. *f. 1–3*. 29 Ja [13 F] 1943.

MORPHOLOGY

(including anatomy, and cytology in part)

Angelo, E., Brown, R. T. & Ammen, H. J. Pollination studies with tung trees. Proc. Am. Soc. Hort. Sci. **41**: 176–180. S 1942.

Bloch, R. Differentiation in red root-tips of *Phalaris arundinacea*. Bull. Torrey Club **70**: 182, 183. *f. 1*. 1 Mr 1943.

Cheadle, V. I. The origin and certain trends of specialization of the vessel in the Monocotyledoneae. Am. Jour. Bot. **30**: 11–17. *f. 1–9*. Ja 1943. [25 F 1943].

Duncan, R. E. & Curtis, J. T. Growth of fruits in *Cattleya* and allied genera in the Orchidaceae. Bull. Torrey Club **70**: 104–119. *f. 1–28*. 1 Mr 1943.

Foster, A. S. Zonal structure and growth of the shoot apex in *Microcycas calocoma* (Miq.) A. DC. Am. Jour. Bot. **30**: 56–73. *f. 1–16*. Ja 1943 [25 F 1943].

Helmers, A. E. The ecological anatomy of ponderosa pine needles. Am. Midl. Nat. **29**: 55–71. Ja 1943 [6 Mr 1943].

Kozlowski, T. T. & Schumacher, F. X. Estimation of stomated foliar surface of pines. Plant Physiol. **18**: 122–127. *1 f*. Ja 1943.

LaRue, C. D. Regeneration in *Radicula aquatica*. Pap. Mich. Acad. **28**[1] (1942): 51–61. F 1943.

Lewis, F. T. A geometric accounting for diverse shapes of 14-hedral cells: the transition from dodecahedra to tetrakaidecahedra. Am. Jour. Bot. **30**: 74–81. *f. 1–7*. Ja 1943 [15 F 1943].

McKay, J. W. Self-sterility in the Chinese chestnut (*Castanea mollissima*). Proc. Am. Soc. Hort. Sci. **41**: 156–160. S 1942.

Mehlquist, G. A. L. Seed production in *Primula obconica*. Proc. Am. Soc. Hort. Sci. **41**: 378–380. S 1942.

Schall, W. M. An investigation of the presence of siliceous rods in the secondary wall of woody tissues. Madroño **7**: 8–14. 28 Ja 1943.

Schroeder, C. A. Pollen germination in the avocado. Proc. Am. Soc. Hort. Sci. **41**: 181, 182. S 1942.

Sinclair, W. B. & Lindgren, D. L. Ridges and sectors induced in the rind of

citrus fruits by fumigation with hydrocyanic acid. Plant Physiol. **18**: 99–106. *f. 1–4.* Ja 1943.

Swanson, C. P. Differences in meiotic coiling between *Trillium* and *Tradescantia*. Pap. Mich. Acad. **28**[1] (1942): 133–142. *pl. 1 + f. 1.* F 1943.

Warmke, H. E. Macrosporogenesis, fertilization, and early embryology of *Taraxacum kok-saghyz*. Bull. Torrey Club **70**: 164–174. *f. 1–33.* 1 Mr 1943.

Woodcock, E. F. Seed development in the morning-glory (*Ipomoea rubrocaerulea* Hook.) Pap. Mich. Acad. **28**[1] (1942): 209–212. *pl. 1–3.* F 1943.

PLANT PHYSIOLOGY

(See also under Mycology and Phytopathology: **Alben, Hammar & Sitton; Rodenhiser & Taylor;** under Morphology: **Duncan & Curtis; La Rue**

Airola, E. & Crist, J. W. Oxidation-reduction potentials of the tissue fluid of cabbage. Plant Physiol. **18**: 107–113. *f. 1–2.* Ja 1943.

Albaum, H. G. & Eichel, B. The relationship between growth and metabolism in the oat seedling. Am. Jour. Bot. **30**: 18–22. *f. 1–7.* Ja 1943 [25 F 1943].

Aldrich, W. W. *et al.* Some factors affecting rate of date leaf elongation. Proc. Am. Soc. Hort. Sci. **41**: 77–84. *f. 1–5.* S 1942.

Avery, G. S. Control of growth and differentiation in plants. Cold Spring Harbor. Symp. Quant. Biol. **10**: 1–6. 1942.

Bonner, J. Further experiments on the nutrition of isolated tomato roots. Bull. Torrey Club **70**: 184–189. 1 Mr 1943.

Carroll, J. C. Effects of drought, temperature and nitrogen on turf grasses. Plant Physiol. **18**: 19–36. *1 f.* Ja 1943.

Cochran, H. L. The carotene content of sweet potatoes. Proc. Am. Soc. Hort. Sci. **41**: 259–264. S 1942.

Commoner, B., Fogel, S. & Muller, W. H. The mechanism of auxin action. The effect of auxin on water absorption by potato tuber tissue. Am. Jour. Bot. **30**: 23–28. *f. 1–5.* Ja 1943 [25 F 43].

Converse, C. D., Gammon, N. & Sayre, J. D. The use of ion exchange materials in studies on corn nutrition. Plant Physiol. **18**: 114–121. *f. 1–3.* Ja 1943.

Cooper, W. C. Effect of growth substances on flowering of the pineapple under Florida conditions. Proc. Am. Soc. Hort. Sci. **41**: 93–98. *f. 1.* S 1942.

Delisle, A. L. Histological and anatomical changes induced by indolacetic acid in rooting cuttings of *Pinus strobus* L. Va. Jour. Sci. **3**: 118–124. My 1942 [Mr 1943].

Epstein, E. & Lilleland, O. A preliminary study of the manganese content of the leaves of some deciduous fruit trees. Proc. Am. Soc. Hort. Sci. **41**: 11–18. *f. 1.* S 1942.

Gossard, A. C. Root and shoot production of young pecan trees treated with indolebutyric acid at the time of transplanting. Proc. Am. Soc. Hort. Sci. **41**: 161–166. *f. 1–2.* S 1942.

Hammer, K. C. Hormones and photoperiodism. Cold Spring Harbor Symp. Quant. Biol. **10**: 49–60. *f. 1–10.* 1942.

Howlett, F. S. Fruit set and development from pollinated tomato flowers treated with indolebutyric acid. Proc. Am. Soc. Hort. Sci. **41**: 277–281. S 1942.

Kersten, H. J., Miller, H. L. & Smith, G. F. Stimulative effects of x-rays on plants. Plant Physiol. **18**: 8–18. *f. 1–11.* Ja 1943.

Jones, W. W. & Shaw, L. The process of oil formation and accumulation in the *Macadamia*. Plant Physiol. **18**: 1–7. Ja 1943.

Levine, M. & Gelber, S. The metaphase stage in colchicinized onion root-tips. Bull. Torrey Club **70**: 175–181. 1 Mr 1943.

Lillebrand, O. & Brown, J. G. The phosphate nutrition of fruit trees IV. The phosphate content of peach leaves from 130 orchards in California and some factors which may influence it. Proc. Am. Soc. Hort. Sci. **41**: 1–10. S 1942.

Lineberry, R. A. & Burkhart, L. The vitamin C content of small fruits. Proc. Am. Soc. Hort. Sci. **41**: 198–200. S 1942.

Pratt, R. Studies on *Chlorella vulgaris* VI. Retardation of photosynthesis by a growth inhibiting substance from *Chlorella vulgaris*. Am. Jour. Bot. **30**: 32, 33. *f. 1–2*. Ja 1943 [25 F 1943].

Robbins, W. J. & Ma, R. The relation of certain fungi to thiamine. Bull. Torrey Club **70**: 190–197. *f. 1–3*. 1 Mr 1943.

Robbins, W. J. & Ma, R. Vitamin deficiencies of twelve fungi. Arch. Biochem. **1**: 219–229. *illust.* D 1942.

Sakr, E. S. & Thompson, H. C. Effect of temperature and photoperiod on seedstalk development in carrots. Proc. Am. Soc. Hort. Sci. **41**: 343–346. S 1942.

Schroeder, R. A. Some effects of calcium and nitrogen upon peas. Proc. Am. Soc. Hort. Sci. **41**: 375–377. S 1942.

Seifriz, W. Protoplasmic streaming. Bot. Rev. **9**: 49–123. F 1943.

Stephenson, R. B. Effects of certain growth regulating substances on growth correlation in lettuce seedlings. Plant Physiol. **18**: 37–50. *f. 1–9*. Ja 1943.

Swanson, C. A. The effect of culture filtrates on respiration in *Chlorella vulgaris*. Am. Jour. Bot. **30**: 8–11. *f. 1, 2*. Ja 1943 [25 F 1943].

Swanson, C. A. Transpiration in American holly in relation to leaf structure. Ohio Jour. Sci. **43**: 43–46. Ja 1943.

Went, F. W. Effect of the root system on tomato stem growth. Plant Physiol. **18**: 51–65. *f. 1, 2*. Ja 1943.

White, P. R. Further evidence on the significance of glycine, pyridoxine and nicotinic acid in the nutrition of excised tomato roots. Am. Jour. Bot. **30**: 33–36. *f. 1–3*. Ja 1943 [25 F 1943].

Wynd, F. L. Respiration of mosaic-infected tobacco plants. Plant Physiol. **18**: 90–98. *1 f.* Ja 1943.

Zimmerman, F. W. Formative influences of growth substances in plants. Cold Spring Harbor Symp. Quant. Biol. **10**: 152–159. *f. 1–4*. 1942.

GENETICS
(including cytogenetics)

(See also under Morphology: **Swanson**; under Plant Physiology: **Levine & Gelber**)

Burton, G. W. Interspecific hybrids in the genus *Paspalum*. Jour. Hered. **34**: 15–23. *f. 9–10*. Ja 1943.

Dale, E. E. Further studies of inheritance of variegation in petunia: broken-variegated. Pap. Mich. Acad. **28**[1] (1942): 9–14. *pl. 1*. F 1943.

Garber, E. The rate of root elongataion in diploid and tetraploid Sudan grass and rye. Am. Nat. **77**: 190–192. [15] Mr 1943.

Johnson, B. L. & Rogler, G. A. A cyto-taxonomic study of an intergeneric hybrid between *Oryzopsis hymenoides* and *Stipa viridula*. Am. Jour. Bot. **30**: 49–56. *f. 1–40*. Ja 1943 [25 F 1943].

Lindegren, C. C. & Lindegren, G. Environmental and genetical variations in yield and colony size of commercial yeasts. Ann. Mo. Bot. Gard. **30**: 71–82. *pl. 2–3 + f. 1–3*. 22 Mr 1943.

Perry, B. A. Cytological relationships in the Euphorbiaceae. Va. Jour. Sci. **3**: 140–144. My 1942. [My 1943]

Stakman, E. C. *et al.* Genetic factors for mutability and mutant characters in *Ustilago zeae.* Am. Jour. Bot. **30:** 37–48. *f. 1–7.* Ja 1943 [25 F 1943].

Stewart, R. M. & Bamford, R. The nature of polyploidy in *Lilium tigrinum.* Am. Jour. Bot. **30:** 1–7. *f. 1–17.* Ja 1943 [25 F 1943].

Walker, M. N. A useful pollination method for watermelon. Jour. Hered. **34:** 11–14. *f. 6–8.* Ja 1943.

Whitaker, T. W. & Pryor, D. E. Genes for resistance to powdery mildew in *Cucumis melo.* Proc. Am. Soc. Hort. Sci. **41:** 270–272. S 1942.

Yarnell, S. H. Influence of the environment on the expression of hereditary factors in relation to plant breeding. Proc. Am. Soc. Hort. Sci. **41:** 398–411. S 1942.

MYCOLOGY AND PHYTOPATHOLOGY

(See also under Genetics: **Whitaker & Pryor**)

Alben, A. O., Hammar, H. E. & Sitton, B. G. Some nutrient deficiency symptoms of the pecan. Proc. Am. Soc. Hort. Sci. **41:** 53–60. S 1942.

Bain, D. C. & Edgerton, C. W. The zonate leaf spot, a new disease of sorghum. Phytopathology **33:** 220–226. *f. 1, 2.* Mr 1943.

Baxter, D. V. Some resupinate polypores from the region of the Great Lakes. XIV. Pap. Mich. Acad. **28**[1] (1942): 215–233. *pl. 1–6.* F 1943.

Bessey, E. A. Notes on Hawaiian fungi. Pap. Mich. Acad. **28**[1] (1942): 3–8. F 1943.

Blodgett, E. C. Peach wart. Phytopathology **33:** 21–32. *f. 1–3.* Ja 1943.

Braun, A. C. & White, P. R. Bacteriological sterility of tissues derived from secondary crown-gall tumors. Phytopathology **33:** 85–100. *f. 1, 2.* F 1943.

Bremer, H. An American oat disease found in western Anatolia. Phytopathology **33:** 165–167. *f. 1–2.* F 1943.

Chilton, S. J. P. Variations in sporulation of different isolates of *Colletotrichum destructivum.* Mycologia **35:** 13–20. *f. 1, 2.* 1 F 1943.

Clayton, E. E. & Stevenson, J. A. *Peronospora tabacina* Adam, the organism causing blue mold (downy mildew) disease of tomato. Phytopathology **33:** 101–113. F 1943.

Cooley, J. S. & Lincoln, F. B. A disease of apple grafts and layers caused by a *Rhizoctonia.* Phytopathology **33:** 255–257. *f. 1.* Mr 1943.

Cutter, V. M. An undescribed *Lagenidium* parasitic upon *Potamogeton.* Mycologia **35:** 2–12. *f. 1–21.* 1 F 1943.

Drechsler, C. Another hyphomycetous fungus parasitic on *Pythium* oospores. Phytopathology **33:** 227–233. *f. 1.* Mr 1943.

Drosdoff, M. & Painter, J. H. A chlorosis and necrosis of tung leaves associated with low potassium content. Proc. Am. Soc. Hort. Sci. **41:** 45–51. *f. 1.* S 1942.

Evans, A. W. Asahina's microchemical studies on the *Cladoniae.* Bull. Torrey Club **70:** 139–151. 1 Mr 1943.

Exner, B. & Chilton, S. J. P. Cultural differences among single basidiospore isolates of *Rhizoctonia solani.* Phytopathology **33:** 171–174. *f. 1.* F 1943.

Gottlieb, D. The presence of a toxin in tomato wilt. Phytopathology **33:** 126–135. *f. 1–4.* F 1943.

Hahn, C. G. Taxonomy, distribution, and pathology of *Phomopsis occulta* and *P. juniperovora.* Mycologia **35:** 112–129. *f. 1, 2.* 1 F 1943.

Hardison, J. R. The occurrence of amphispores in the leaf rust of bluegrasses. Mycologia **35:** 79–82. *f. 1, 2.* 1 F 1943.

Hildebrand, E. M. Peach-suture spot. Phytopathology **33**: 167, 168. *f. 1*. F 1943.

Holton, C. S. & Johnson, A. G. Physiologic races in *Urocystis tritici*. Phytopathology **33**: 169–171. F 1943.

Immer, F. R., Christensen, J. J. & Loegering, W. Q. Reactions of strains and varieties of barley to many physiologic races of stem rust. Phytopathology **33**: 253–254. Mr 1943.

Jenkins, A. E. Additional records of violet scab. Phytopathology **33**: 168, 169. F 1943.

Linder, D. H. The genera *Kickxella, Martensella,* and *Coemansia* (Phycomycetes). Farlowia **1**: 49–77. *pl. 1–4*. Ja 1943.

Long, W. H. & Stouffer, D. J. Studies in the Gasteromycetes VII. The genus *Schizostoma*. Mycologia **35**: 21–32. *f. 1–8*. 1 F 1943.

Miller, J. H. & Burton, M. G. Studies in some Venezuelan Ascomycetes collected by C. E. Chardon and A. S. Muller. Mycologia **35**: 83–94. *f. 1–10*. 1 F 1943.

Nauss, R. N. Observations on the culture of *Hemitrichia vesparium*, with special reference to its black plasmodial color. Bull. Torrey Club **70**: 152–163. *f. 1–5*. 1 Mr 1943.

Newhall, A. G. Pathogenesis of *Ditylenchus dipsaci* in seedlings of *Allium cepa*. Phytopathology **33**: 61–69. *f. 1, 2*. Ja 1943.

Nickerson, W. J. *Zygosaccharomyces acidifaciens*: a new acetifying yeast. Mycologia **35**: 66–78. *f. 1–4*. 1 F 1943.

Pierce, E. C. & Stoddard, D. L. Some effects of sand and nutrient supply on a physiological leaf spot of cantaloupe. Phytopathology **33**: 162–164. F 1943.

Poesch, G. H. Ring spot on *Saintpaulia*. Proc. Am. Soc. Hort. Sci. **41**: 381, 382. S 1942.

Prince, A. E. Basidium formation and spore discharge in *Gymnosporangium nidus-avis*. Farlowia **1**: 79–93. *pl. 1*. Ja 1943.

Rodenhiser, H. A. & Taylor, J. W. The effect of photoperiodism on the development of bunt in two spring wheats. Phytopathology **33**: 240–244. Mr 1943.

Rogers, D. P. The genus *Pellicularia* (Thelephoraceae). Farlowia **1**: 95–118. *f. 1–11*. Ja 1943.

Ryker, T. C. Physiologic specialization in *Cercospora oryzae*. Phytopathology **33**: 70–74. *f. 1*. Ja 1943.

Schiel, E. & Marco, P. R. Influencia de la infección de la soja con *Rhizobium japonicum*, sobre el rendimiento y calidad del forraje. Rev. Arg. Agron. **9**: 284–291. D 1942.

Seaver, F. J. *Dictyophora duplicata*. Mycologia **35**: 1. *front*. 1 F 1943.

Seeler, E. V. Several fungicolous fungi. Farlowia **1**: 119–133. *pl. 1–2*. Ja 1943.

Singer, R. & Smith, A. H. A monograph on the genus *Leucopaxillus Boursier*. Pap. Mich. Acad. **28**[1] (1942): 85–132. *pl. 1–8*. F 1943.

Smith, A. L. Lightning injury to cotton. Phytopathology **33**: 150–155. *f. 1–2*. F 1943.

Smith, W. W. Development of the storage disorder brown core in McIntosh apples. Proc. Am. Soc. Hort. Sci. **41**: 99–103. S 1942.

Tapke, V. F. Occurrence, identification, and species validity of the barley loose smuts, *Ustilago nuda, U. nigra,* and *U. medians*. Phytopathology **33**: 194–209. *f. 1–4*. Mr 1943.

Thomas, H. R. *Cercospora* blight of carrot. Phytopathology **33**: 114–125. *f. 1–2*. F 1943.

Thomas, W. D. Mycorhizae associated with some Colorado flora. Phytopathology **33**: 144–149. *f. 1.* F 1943.

Valleau, W. D. & Johnson, E. M. An outbreak of *Plantago* virus in burley tobacco. Phytopathology **33**: 210–219. *f. 1, 2.* Mr 1943.

Waksman, S. A. & Horning, E. S. Distribution of antagonistic fungi in nature and their antibiotic action. Mycologia **35**: 47–65. *f. 1–7.* 1 F 1943.

Weimer, J. L. Anthracnose of lupines. Phytopathology **33**: 249–252. *f. 1.* Mr 1943.

Wellman, F. L. Increase of pathogenicity in tomato-wilt *Fusarium*. Phytopathology **33**: 175–193. *f. 1, 2.* Mr 1943.

White, W. L. Studies in the genus *Helotium*, III (Discomycetes). History and diagnosis of certain European and North American foliicolous species. Farlowia **1**: 135–170. *f. 1–17.* Ja 1943.

Zeller, S. M. & Braun, A. J. Decline disease of raspberry. Phytopathology **33**: 156–161. *f. 1, 3.* F 1943.

Zeller, S. M. & Braun, A. J. Stamen blight of blackberries. Phytopathology **33**: 136–143. *f. 1–3.* F 1943.

PALEOBOTANY

Andrews, H. N. Notes on the genus *Tempskya*. Am. Midl. Nat. **29**: 133–136. *pl. 1.* Ja 1943 [6 Mr 1943].

Andrews, H. N. & Lenz, L. W. A mycorrhizome from the Carboniferous of Illinois. Bull. Torrey Club **70**: 120–125. *f. 1–8.* 1 Mr 1943.

Cain, S. A. A note on "Fossil evidence of wider post-pleistocene range for butternut and hickory in Wisconsin." Rhodora **45**: 107–109. 17 Mr 1943.

Hansen, H. P. A pollen study of a subalpine bog in the Blue Mountains of northeastern Oregon. Ecology **24**: 70–78. Ja 1943.

Janson, E. & Halfert, E. Pollen analysis of a Swedish bog near Lake Stor-Uman. Pap. Mich. Acad. **28**[1] (1942): 41–45. *f. 1, 2.* F 1943.

Johnson, J. H. Geologic importance of calcareous algae with annotated bibliography. Quart. Colorado School Mines **38**: 1–102. *f. 1–23.* Ja 1943.

Kosanke, R. M. The characteristic plant microfossils of the Pittsburgh and Pomeroy coals of Ohio. Am. Midl. Nat. **29**: 119–132. *pl. 1–3.* Ja 1943 [6 Mr 1943].

Rosendahl, C. O. Some fossil fungi from Minnesota. Bull. Torrey Club **70**: 126–138. *f. 1–20.* 1 Mr 1943.

ECOLOGY AND PLANT GEOGRAPHY

(See also under Plant Physiology: **Carroll**)

Bauer, H. L. The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology **24**: 45–60. Ja 1943.

Buell, M. F. & Cain, R. L. The successional rôle of southern white cedar, *Chamaecyparis thyoides*, in southeastern North Carolina. Ecology **24**: 85–93. *f. 1–4.* Ja 1943.

Cobbe, T. J. Variations in the Cabin Run Forest, a climax area in southwestern Ohio. Am. Midl. Nat. **29**: 89–105. *f. 1–9.* Ja 1943 [6 Mr 1943].

Kenoyer, L. A. Forest associations of Ottawa County, Michigan, at the time of the original survey. Pap. Mich. Acad. **28**[1] (1942): 47–50. *f. 1.* F 1943.

McClure, H. E. Aspection in the biotic communities of the Churchill area, Manitoba. Ecol. Monog. **13**: 1–35. *f. 1–24.* Ja 1943.

Odum, E. P. The vegetation of the Edmund Niles Huyck Preserve, New York. Am. Midl. Nat. **29**: 73–88. Ja 1943 [6 Mr 1943].

Smith, N. F. A study of the spread of forest cover into wild-land openings. Pap. Mich. Acad. **28**¹ (1942): 269–277. F 1943.

Stahelin, R. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology **24**: 19–30. *f. 1–3.* Ja 1943.

Walp, R. L. Ecology of Indian Run Ridge. Jour. Gray Mem. Bot. Assoc. **10**: 6–9. *4. f.* Ja 1943.

Weaver, J. E. & Albertson, F. W. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecol. Monogr. **13**: 63–117. *pl. 1–7.* Ja 1943.

GENERAL BOTANY
(including biography)

Apolinar Maria, H. Vocabulario de terminos vulgares en historia natural Colombiana. Rev. Acad. Colombiana **5**¹⁷: 40–60. Ja–Je 1942.

Bartram, J. Diary of a journey through the Carolinas, Georgia, and Florida from July 1, 1765, to April 10, 1766 annotated by Francis Harper. Trans. Am. Philos. Soc. NS **33**¹: 1–120. *pl. 1–22.* D 1942.

Blomquist, H. L. & Pyron, J. H. Drifting "seaweed" at Beaufort, North Carolina. Am. Jour. Bot. **30**: 28–32. *f. 1–2.* Ja 1943 [25 F 1943].

Chapman, V. J. The aims of future research in the algae. Farlowia **1**: 5–8. Ja 1943.

Curtis, J. T. An unusual pollen reaction in *Phalaenopsis.* Am. Orchid Soc. Bull. **11**: 258–260. *1 pl.* 7 Ja 1943.

Dodd, J. D. & Gershoy, A. Experiments in the grafting of species in the genus *Viola.* Bull. Torrey Club **70**: 91–103. 1 Mr 1943.

McVaugh, R. The travels of Thomas Coulter, 1824–1827. Jour. Wash. Acad. **33**: 65–70. *f. 1.* 15 Mr 1943.

Record, S. J. & Hess, R. W. Timbers of the new world. xvi, 1–640. *illust.* New Haven, Yale Univ. Press, 1943.

Tsudy, R. H. & Sargent, M. C. Agar-bearing seaweeds at La Jolla, California. Science **97**: 89, 90. 22 Ja 1943.

Tucker, J. M. Francesco Franceschi. Madroño **7**: 18–27. *port.* 28 Ja 1943.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 335–348 . JULY, 1943

THE SHOOT APICES OF ATHROTAXIS AND TAIWANIA[1]

G. L. CROSS

INTRODUCTION

It has been demonstrated that the apical meristem in seed plants does not consist of a homogeneous aggregation of cells, but that it is differentiated into "growth zones" which may be distinguished from each other by differences in cellular size, rate and plane of cellular division, staining reaction, vacuolation, thickness of cell walls and polarity of growth (Foster 1941). The structural and functional relationships of the growth zones in species from several major groups of plants, ranging from the Lycopodiales to the Monocotyledons, have been studied recently, and considerable variation has been reported. Although the various species in a family may possess shoot apices with similar fundamental features of cellular organization, these features are not always found in the species of other, apparently related families and, therefore, homology or equivalence of growth zones in the various groups is difficult to determine (Foster 1939a). Further, many perplexing and seemingly inconsistent differences of detail are sometimes found when the apices of the various species of a genus are compared carefully (Cross 1938, Foster 1939a, Cross and Johnson 1941). And finally, although the structural features of the shoot apices of individuals belonging to the same species are reasonably constant, variation in cellular pattern is often found, and there is good evidence that even a single apex may change markedly during the seasonal development of a shoot (Cross 1943) or in relation to the initiation of foliar primordia (Cross and Johnson 1941, Reeve 1942). The evolution of the apical meristem in the various groups is a puzzling problem which can be solved only when considerable additional information is available.

It seems evident that one step toward the solution of the problem must be the acquisition of information concerning the shoot apices of a considerable number of *species* of plants; i.e., specific information concerning: (1) the fundamental structural features which are characteristic of the apices of representative species belonging to the same taxonomic group; (2) the changes of cellular pattern which occur in the apices of individual plants during a growing season; and (3) the significance of the changes in cellular pattern with respect to the growth of the shoot as a whole. Only after such a comprehensive, detailed survey of species has been made will it be possible to generalize concerning the relationships of the shoot apices in the major taxonomic units. The information should be useful not only to

[1] Contribution from the Botanical Laboratory of the University of Oklahoma n.s. 79.

[THE BULLETIN for May (70: 213–334) was issued April 30, 1943]

students of phylogeny, but to other investigators as well, for it has been shown that knowledge of the apical meristem can be used with unique effectiveness in studying several phases of shoot morphology (Satina and Blakeslee 1941) and in certain fields of experimental genetics (Cross and Johnson 1941, Cross 1943).

In 1939, the writer began a survey of the shoot apices of species from each genus in the Taxodiaceae, and to date *Taxodium distichum* Rich., *Cryptomeria japonica* (L. F.) Don, *Cunninghamia lanceolata* (Lamb.) Hook., *Sequoia sempervirens* (Lamb.) Endl., and *Sequoiadendron giganteum* (Lindl.) Buch. have been studied. Materials for completing the study of the family are on hand, with the exception of apices of *Glyptostrobus*, and it is hoped that shoot tips of this little-known genus may be obtained from the native habitat in southern China, after the war.

The earlier invesigations (Cross 1939, 1941, 1942, 1943) indicate that, although generic and specific differences do exist, there are basic similarities in form and cellular pattern of the shoot apices which may be used to characterize the family. With respect to form, the apices of the investigated genera vary from hemispherical in *Taxodium* and *Cryptomeria* to conical in *Cunninghamia*. The prevailing cellular pattern differs from those reported recently for other genera of the Coniferales (Korody 1937). In each species of the Taxodiaceae the apical meristem has been found to consist of: (1) a single tier of self-perpetuating apical initials, which may divide periclinally as well as anticlinally; (2) a protoderm in which the cells divide strictly anticlinally except that periclinal divisions may occur rarely in at least one species (Cross 1943); (3) a variable number of subapical mother cells in which divisions occur in diverse planes; (4) a ring or cylinder of peripheral meristem; and (5) a core of pith mother cells. The functional relationships of these "growth zones" are reasonably constant in the various species. The apical initials constitute the source from which the remainder of the shoot apex is derived. Lateral derivatives of the apical initials augment the protoderm and basal derivatives become subapical mother cells. Lateral and basal derivatives of the subapical mother cells contribute to the peripheral meristem and pith mother cells respectively.

The main differences found when apices of the various species are compared involve: (1) the extent to which periclinal divisions occur in the apical initials, and (2) the genetic relationships of the cells of the peripheral meristem and the pith mother cells. In most genera the line of demarcation between the peripheral meristem and the pith mother cells is reasonably sharp, however in certain apices of *Cunninghamia* the distinctions are obscure, and occasionally the cells which occupy the *position* of pith mother cells appear to proliferate laterally toward the peripheral meristem (Cross 1942, fig. 10a). Of course, there are differences in size also; the largest shoot apex (diameter 220 μ) measured thus far was from a strong lateral branch

of *Sequoia sempervirens,* and the smallest (diameter 45 μ) was from a weak lateral branch of *Sequoiadendron giganteum.* All measurements were made in a plane equidistant from the summit of the apex and the axil of the youngest foliar primordium.

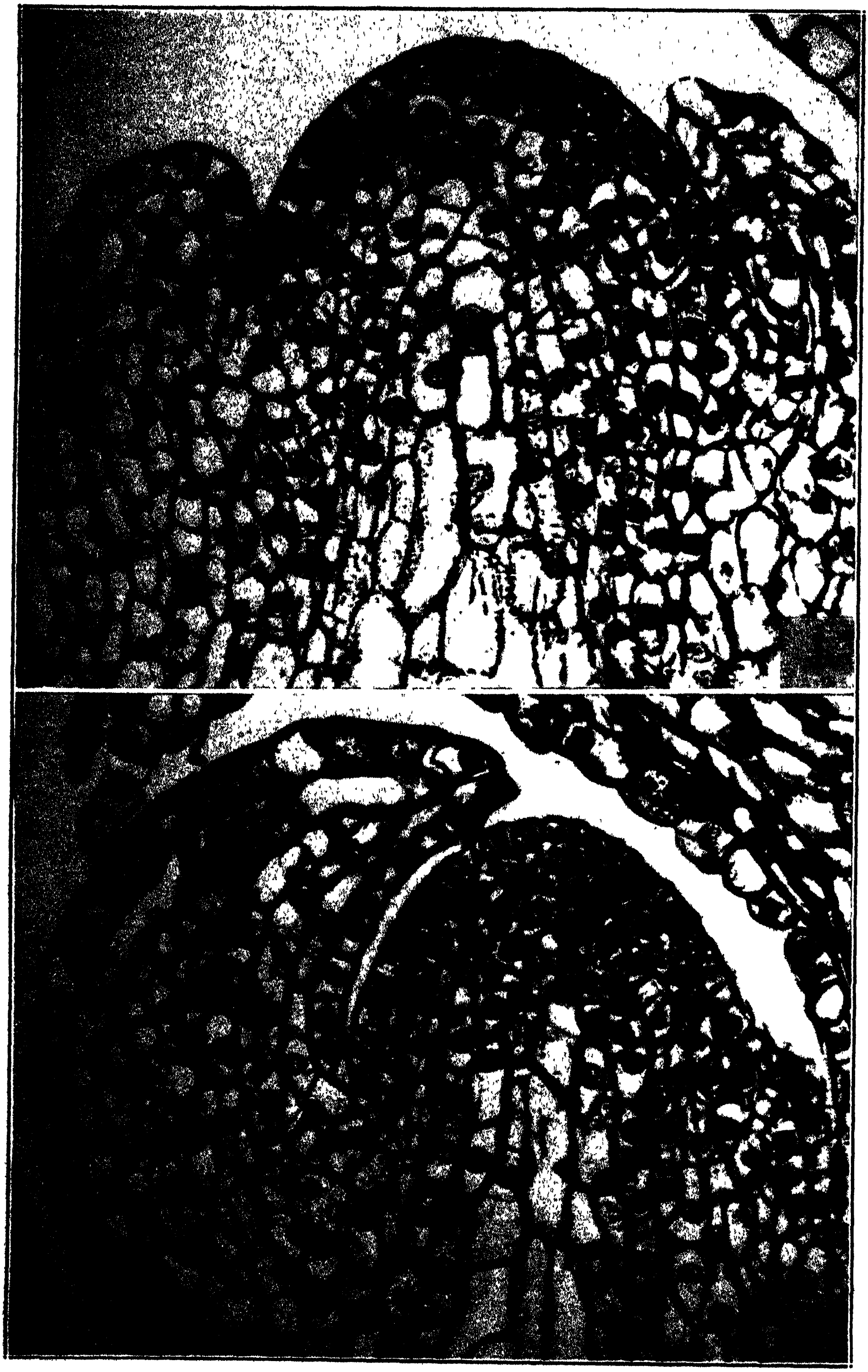
The present study of the shoot apices of *Athrotaxis selaginoides* Don and *Taiwania cryptomerioides* Hayata is confined to a comparison of the fundamental structural features found in these species with the features described previously for other species of the Taxodiaceae. Materials available were limited and it was not thought practicable to attempt a study of seasonal variations in cellular pattern.

METHODS

According to the accounts of Pilger (1926) and Chamberlain (1935), *Athrotaxis* and *Taiwania* are very restricted in natural distribution. *Athrotaxis* apparently occurs only in the mountainous areas of western Tasmania, while *Taiwania* is limited to forested mountains of Formosa and Yünnan. The trees have not been planted extensively in the botanical gardens or parks of the United States and, as might be expected, materials for study were very difficult to obtain.

However, through the kindness of Professor John T. Buchholz, a limited number of shoots of *Athrotaxis* were obtained from a plant—possibly the only living specimen in the United States—growing in a private garden near Golden Gate Park, San Francisco. Professor Buchholz had preserved the branchlets in formalin-acetic-ethyl alcohol. Grateful acknowledgment is made also to Dr. William Hertrich, Curator of the Huntington Botanical Gardens at San Marino, California, who supplied a number of fresh shoots of *Taiwania.* These were fixed by the writer under reduced pressure in a mixture of 5 per cent commercial formalin and 6 per cent glacial acetic acid, made up in 70 per cent ethyl alcohol.

The materials were processed and the illustrations prepared as described in previous papers (Cross 1937, 1939, 1940). Although all of the materials were processed in essentially the same manner, the end results were quite different, especially so with respect to staining reactions. The cytoplasm in the cells of *Athrotaxis* stained very lightly (figs. 1, 2) when safranin and fast green were applied, but in *Taiwania* the cytoplasm stained densely, so much so as to interfere with satisfactory differentiation (figs. 3–6). Perhaps this phenomenon was a result of differences in the degree of activity of the meristem of the two genera, or perhaps killing and fixation may have been less rapid in the larger apices of *Taiwania.* Fixation of the cells of *Athrotaxis* was generally satisfactory, but considerable plasmolysis occurred in those of *Taiwania.* Perhaps the cytoplasm of *Taiwania* stained more densely because the vacuoles had been reduced in size by the plasmolyzing action of the fixing reagents.



GENERAL FEATURES OF THE VEGETATIVE SHOOTS

Both species are trees; according to Pilger (1926), *A. selaginoides* attains a height of 13–15 meters and is strongly branched, while *T. cryptomerioides* may reach 50 meters and is branchless for about one-half of its height.

The vegetative shoots of *Athrotaxis* consist of sturdy, rigid axes upon which the leaves are born in a loose, spiral arrangement which often appears imbricate. The leaves are persistent, leathery, awl-shaped or lanceolate, and keeled on the abaxial surface. According to Pilger (1926) the leaves may grow to a length of 1 cm., but the basal portions (approximately one-half of each leaf) are undiverged from the shoot axis. Bud scales are not found on the vegetative shoots, but the leaves which have formed the outer constituents of dormant buds are usually considerably smaller than the others and, therefore, it is easy to determine the limits of the yearly growth-increments.

The vegetative shoots of *Taiwania* resemble those of *Athrotaxis* in that they consist of rigid stems and spirally arranged leaves. The leaves from the lower portions of a tree or from a young plant (Pilger 1926) are from linear to needle-shaped, very stiff and sharp, laterally flattened, and keeled on both the abaxial and adaxial surfaces. They may be as long as 15 mm., but a broad, basal portion of each leaf is undiverged from the shoot axis. Leaves from the upper portions of a tree are much shorter and scale-like. They are quite thick and appear triangular when viewed from the upper or lower surface. The adaxial keel is usually reduced, and in some instances the upper surfaces of the leaves may be slightly concave, with inwardly turned tips. Bud scales are not found.

STRUCTURAL FEATURES OF THE SHOOT APICES

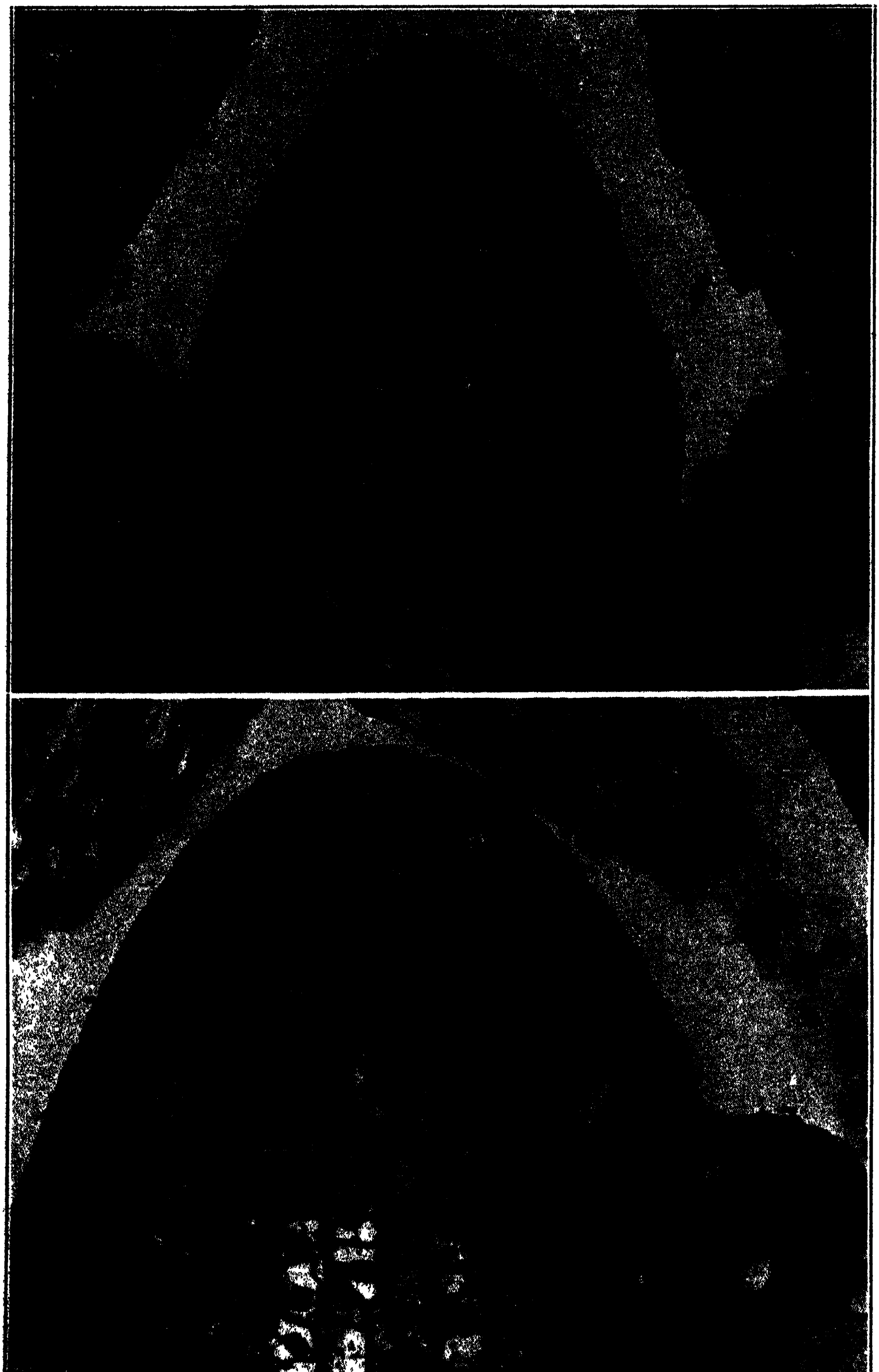
Although the literature was searched carefully, no reference to the shoot apices of either *Athrotaxis* or *Taiwania* was found. However, the results of this investigation indicate definitely that the apical meristem in each of these genera is characterized by the same fundamental features of organization that have been described for other representatives of the Taxodiaceae. As a matter of fact, the similarities are so marked that detailed descriptions of the apices of *Athrotaxis* and *Taiwania* will not be necessary—only a brief comparative treatment need be given.

The apices of *Athrotaxis* are hemispherical and, with respect to form, resemble those of *Cryptomeria* (Cross 1941). They vary in diameter from 65 to 120 μ, measured in a plane equidistant from the shoot tip and the axil of the youngest leaf. They rank, therefore, with those of *Cryptomeria* and

---

Explanation of figures 1, 2.

FIG. 1. Nearly median longisection of shoot apex and foliar primordium of *Athrotaxis*. × 484. FIG. 2. Nearly median longisection of shoot apex and older leaf of *Athrotaxis*. Note continuity of protoderm on flank of apex and over the leaf. × 484.



the lateral shoots of *Sequoiadendron* (Cross 1943), among the smallest recorded for the Taxodiaceae. On the other hand, the apices of *Taiwania* are conical and appear parabolic in longisection like those of *Cunninghamia* (Cross 1942). They are somewhat more massive, and a range in diameter of from 90 to 160 μ was found in the twenty-five shoot tips which were measured. An idea of the variation in size and form may be obtained from a careful comparison of figures 1–6. The structural features of the apices of the two genera are discussed in the following paragraphs.

The Apical Initials. The summit of the apical meristem consists of a single tier of self-perpetuating apical initials which divide periclinally as well as anticlinally and, although 25 apices of each species were examined, no indication of a discrete surface layer over the tip of the apical meristem was found (figs. 1, 2, 3–6). Apparently the periclinal and anticlinal divisions occur with approximately equal frequencies, and in this respect the apices of *Athrotaxis* and *Taiwania* resemble those of *Cunninghamia* (Cross 1942). Occasionally an oblique division may produce a triangular apical cell (fig. 4) suggestive of those found regularly in the shoot tips of many species of leptosporangiate ferns. Doubtless Korschelt's (1884) report of an apical cell in the shoot tips of *Taxodium* was based upon studies of sections similar to the one represented by figure 4. However, it seems evident that this phenomenon occurs infrequently, and the cellular pattern which results is transitory. As in other species of the Taxodiaceae, but unlike those of the Abietaceae, lateral derivatives of the apical initials differentiate into a protoderm; the basal derivatives become subapical mother cells.

The Protoderm. The presence of a protoderm on the flanks and lower shoulders of the apical meristem has been demonstrated for each of the investigated species of Taxodiaceae. In this layer mitotic figures are almost always oriented parallel with the surface of the meristem, and in the apices of *Athrotaxis* and *Taiwania* the resulting uniseriate layer is clearly delimited from the underlying tissue by a thicker, more heavily staining wall which can be traced down the flanks of the apical meristem and over the tips of the foliar primordia. This feature is usually conspicuous in the apices of *Athrotaxis* (figs. 1, 2), but it may be observed without difficulty in those of *Taiwania* (figs. 3–6). Periclinal divisions in the protoderm have been reported to occur rarely in *Sequoia sempervirens* (Cross 1943) and in *Sciadopitys* (Strasburger 1872) on the flanks of the apical meristem, but they have not been reported to occur during foliar initiation in any species of the

Explanation of figures 3, 4.

FIG. 3. Nearly median longisection of apex of a smaller lateral shoot of *Taiwania*. Note sequence of walls in the apical initials. × 484. FIG. 4. Nearly median longisection of apex of a more vigorous shoot of *Taiwania*. Note triangular "apical cell" at the summit. × 484.

Taxodiaceae. In this respect the apices of the Taxodiaceae contrast sharply with those of the Abietaceae (Korody 1937) but are comparable with those of *Araucaria* and *Ephedra* (Strasburger 1872).

The Subapical Mother Cells. Subapical mother cells, arising from the inner derivatives of the subapical initials, are of common occurrence in the Gymnosperms. They exist, at least theoretically in all species which have periclinally dividing apical initials, although their delimitation from other subterminal growth zones (peripheral meristem and pith mother cells) may not always be well marked. In *Athrotaxis* and *Taiwania,* as in other genera, they are distinguished by their position, their diversity with respect to planes of cellular division, and to a lesser extent by their inconspicuous vacuolation. Considerable quantitative variation is noticed when individual apices are studied. Thus in figure 1 the zone of subapical mother cells is limited vertically, and the pith mother cells extend to within a very few cell layers of the summit of the axis. In figure 2 this zone has a greater vertical extension, and the pith mother cells are differentiated much lower in the shoot tip. The reasons for these variations are not understood.

During the investigation it was noticed that the nuclei in the shoot apices of *Athrotaxis* appear to be smaller than those of *Taiwania,* although similar differences in cellular size were not so apparent. Twenty-five nuclei from each genus were measured, using a camera lucida and a card ruler drawn to the proper scale, and it was found that the nuclei of *Athrotaxis* are from 6 to 7 μ in diameter, whereas those of *Taiwania* are from 9 to 10 μ. An equal number (25) of major and minor cellular dimensions were also determined for the subapical mother cells of each genus. The cells of *Athrotaxis* averaged approximately $9 \times 15\ \mu$, those of *Taiwania* $10 \times 15\ \mu$. While these measurements are only approximations, they give evidence that the ratio of the nuclear volume to cellular volume is somewhat less in *Athrotaxis* than in *Taiwania.* The photomicrographs also provide evidence for this suggestion. A careful statistical study of these features, made by someone to whom adequate cytological materials are available. might be worthwhile.

Lateral derivatives of the subapical mother cells produce the peripheral meristem, while basal derivatives differentiate into pith mother cells.

The Peripheral Meristem. The peripheral meristem is arranged in the form of a ring or cylinder which surrounds the pith mother cells. The limits between this zone and the subapical mother cells is often vague, especially in the smaller apices (figs. 2, 3); however, the cellular divisions in the peripheral meristem are prevailingly anticlinal, and therefore the derivatives

Explanation of figures 5, 6.

Nearly median longisections of the apices of vigorously growing shoots of *Taiwania.* $\times 484$.

are arranged in strata. The number of layers varied from two to three in *Athrotaxis* and from two to four in *Taiwania*. No unusual developmental features were observed. Derivaties of the peripheral meristem become vascular tissue, cortical tissue, and the internal portions of leaves.

The Pith Mother Cells. The pith mother cells are distinguishable at a variable distance (from 3 to 5 cell layers) below the summit of the axis. In *Athrotaxis* they divide once or twice, preponderately in transverse planes, thus forming short vertical files of two or three cells. These cells then gradually enlarge and mature into pith (figs. 1, 2). In *Taiwania* the behavior is similar, although here the files of cells derived from the pith mother cells are sometimes longer, occasionally consisting of four or five cells (figs. 4–6). Enlargement and maturation of these derivatives into pith proceeds at a slower rate than in *Athrotaxis*, therefore mature pith is usually found at a considerably greater distance from the shoot tip. Thus, as in other genera of the Taxodiaceae, an extensive rib meristem is not formed. This is a second feature which contrasts with the situation reported for certain genera of the Abietaceae (Korody 1937), *Zamia* (Johnson 1939), *Cycas* and *Dioon* (Foster 1941) and *Ginkgo* (Foster 1938).

DISCUSSION

The shoot apices of representative species of all genera of the Taxodiaceae except *Sciadopitys* and *Glyptostrobus* have been examined during the past three years. In a recent paper (Cross 1943) it has been suggested that there are basic structural features which characterize the family, because in all investigated species the apical meristem consists of apical initials, a protoderm, subapical mother cells, peripheral meristem, and pith mother cells. The data obtained from the apices of *Athrotaxis* and *Taiwania* support this tentative conclusion.

Self-perpetuating apical initials occur (at least theoretically) in all shoot apices. In the more "primitive" groups, such as the Lycopodiales, Cycadales, and Abietaceae, these initials may divide anticlinally, periclinally or obliquely (Härtel 1938, Foster 1941, Korody 1937). In the more "advanced" groups (Angiosperms) only anticlinal divisions occur in the majority of cases, although Sharman (1940) has shown that exceptions may occur. In the Taxodiaceae the apices of several genera (*Taxodium, Cryptomeria,* and *Sequoia*) show evidence of a reduction in the relative number of periclinal and oblique divisions that occur. Whether this indicates an evolutionary trend toward the development of a discrete surface layer (tunica) in the family remains to be seen.

The occurrence of a protoderm appears to be a relatively "advanced" characteristic, although it is not unique among gymnospermous genera.

This feature does not appear in the apices of the investigated species of *Lycopodium* (Härtel 1938), the Cycadales (Foster 1941, 1943), and the Abietaceae (Strasburger 1872, Korody 1937), although it has been reported in species of *Araucaria* (Strasburger 1872) and *Ephedra* (Strasburger 1872, Gifford 1943). In the Angiosperms a protoderm occurs prevailingly, although in some monocotyledons this layer has the unique feature of dividing periclinally during foliar initiation, and thereby contributes substantially to the internal portions of the foliage leaves (Rösler 1928, Kliem 1937). The fact that the surface layer of the shoot apices of the Taxodiaceae consists of a protoderm on the flanks, and diversely dividing apical initials at the summit, would indicate that this family represents a condition phylogenetically intermediate between the groups which lack a protoderm (Lycopodiales, Cycadales, and Abietaceae) and those which have an entirely discrete surface layer (most Angiosperms). Of course, this does not mean that the family is to be regarded as a "connecting link" between the Gymnosperms and Angiosperms, for admittedly the phylogenetic relationships of these two groups are still obscure. But it may mean that, with respect to shoot apices, parallel evolutionary processes are occurring.

Any shoot apex in which the apical initials divide periclinally may be interpreted as possessing subapical mother cells, a situation which occurs widely in the Gymnosperms. The characteristics of the subapical mother cells vary markedly when apices of various species are compared or even when apices of the same individual are studied; however, these variations are usually of a quantitative nature. The situation is exceedingly complex in some of the Cycads, especially in *Microcycas* (Foster 1943). Here the derivatives of the surface initials are arranged in long files of cells, a portion of which differentiates into peripheral meristem and the remainder into deeply located "central mother cells." The significance of the specialized subterminal region of the apical meristem of cycads to the evolution of shoot apices in seed plants is one of the most puzzling problems associated with shoot histogenesis. It has been suggested that a clue to the answer may be obtained by comparing the cellular patterns found in some of the more "primitive" apices of the Taxodiaceae, such as *Cunninghamia* (Cross 1942) with those of cycad seedlings (Foster 1939b), although much additional work must be done before conclusive results can be obtained. Perhaps a knowledge of the apices of some of the Angiosperms with growth habits similar to those of the cycads would be of aid. In this connection Boke (1941) and Ball (1941) have made recent contributions concerning cacti and palms respectively.

If periclinal divisions do not occur in the apical initials, as is the case in most Angiosperms, the subjacent tier of cells may be regarded as *subapical initials* because, under such circumstances they would be self-perpetuating. Aside from phylogenetic considerations, the occurrence of subapical initials

is of considerable importance to experimental geneticists, especially those working on problems involving polyploidy (Satina and Blakeslee 1941).

A peripheral meristem is found in the apices of all plants in which medullation occurs at a higher level in the axis than the differentiation of cortical parenchyma. This growth zone occurs commonly in Gymnosperms and has been reported for certain species of small-leaved dicotyledons, including certain cacti (Boke 1941) and *Linum* (Esau 1942). In most Gymnosperms and dicotyledons, derivatives of this zone produce foliar primordia (the internal portions), cortical tissue, and provascular tissue.

Pith mother cells, of course, are found in all vascular plants in which a pith occurs. They arise from initiating regions immediately above in the axis (subapical mother cells or subapical initials). The pith mother cells usually develop into a rib meristem which may extend vertically for a considerable distance as in *Ginkgo,* various cycads, and some conifers (Foster 1938, 1941, Korody 1937) or may be very short as in the Taxodiaceae and some Angiosperms (Esau 1942).

From the above discussion it is clear that the structural features found in the shoot apices of the Taxodiaceae are widely distributed among vascular plants. The chief interest of the family lies in the fact that here the various features may be found combined in a single apex. The most unique single characteristic appears to be that the surface layer consists of cells which divide diversely at the summit (apical initials) and only anticlinally (with rare exceptions) on the lower shoulders and flanks. However, Sharman's (1940) report of a periclinally dividing cell in the surface layer at the summit of the apical meristem of *Zea* minimizes the uniqueness of this feature and emphasizes that differences in cellular patterns are often essentially quantitative, i.e., contingent upon the *frequency* with which deviations from the expected behavior inevitably occur. Thus the shoot apices of the Taxodiaceae differ from those of Angiosperms with respect to only one essential feature, viz., the frequency (greater) with which periclinal divisions occur in the surface layer at the summit. They differ from the apices of the Abietaceae only with respect to the frequency (lesser) with which periclinal divisions occur in the surface layer on the flanks of the meristem, and the extent (lesser) to which divisions occur in the rib meristem. Thus, from a phylogenetic point of view, the "transitional" nature of the apical meristem of the Taxodiaceae seems well established.

SUMMARY

The shoot apices of *Athrotaxis* are hemispherical and, in longisection, resemble those of *Cryptomeria.* They are among the smallest reported for the Taxodiaceae, ranging from 65 to 120 μ in diameter in a plane equidistant from the shoot tip and the axil of the youngest leaf. The apices of *Taiwania*

are conical, 90 to 160 μ in diameter, and reminiscent of those of *Cunninghamia.*

The cellular patterns in each genus resemble those of the previously investigated genera of the Taxodiaceae, and no unusual features were observed. The apical meristem consists of a single tier of self-perpetuating *apical initials;* a *protoderm,* derived from lateral derivatives of the apical initials; *subapical mother cells,* derived from basal derivatives of the apical initials; *peripheral meristem,* derived from lateral derivatives of the subapical mother cells; and *pith mother cells,* derived from basal derivatives of the subapical mother cells. The subterminal growth zones (subapical mother cells, peripheral meristem, and pith mother cells) are rather poorly delimited, especially in the smaller apices of each genus.

With respect to the structural features of the surface layer of the apical meristem, the genera of the Taxodiaceae are regarded as intermediate between the more primitive Gymnosperms (Cycadales and Abietaceae) and the Angiosperms, although this is probably to be regarded as a case of parallel evolution rather than phylogenetic relationship.

DEPARTMENT OF PLANT SCIENCES, UNIVERSITY OF OKLAHOMA
NORMAN, OKLAHOMA

Literature Cited

Ball, E. 1941. The development of the shoot apex and of the primary thickening meristem in *Phoenix canariensis* Chaub., with comparisons to *Washingtonia filifera* Wats. and *Trachycarpus excelsa* Wendl. Am. Jour. Bot. **28**: 820–831.

Boke, N. H. 1941. Zonation in the shoot apices of *Trichocereus spachianus* and *Opuntia cylindrica.* Am. Jour. Bot. **28**: 656–664.

Chamberlain, C. J. 1935. Gymnosperms, Structure and Evolution.

Cross, G. L. 1937. An improved method of staining with fast green. Proc. Okla. Acad. **17**: 69–70.

————. 1938. A comparative histogenetic study of the bud scales and foliage leaves of *Viburnum Opulus.* Am. Jour. Bot. **26**: 246–258.

————. 1939. The structure and development of the apical meristem in the shoots of *Taxodium distichum.* Bull. Torrey Club **66**: 431–452.

————. 1940. Development of the foliage leaves of *Taxodium distichum.* Am. Jour. Bot. **27**: 471–482.

————. 1941. Some histogenetic features of the shoot of *Cryptomeria japonica.* Am. Jour. Bot. **28**: 573–582.

————. 1942. Structure of the apical meristem and development of the foliage leaves of *Cunninghamia lanceolata.* Am. Jour. Bot. **29**: 288–301.

————. 1943. A comparison of the shoot apices of the sequoias. Am. Jour. Bot. **29**: (*in press*).

Cross, G. L., & Johnson, T. J. 1941. Structural features of the shoot apices of diploid and colchicine-induced, tetraploid strains of *Vinca rosea* L. Bull. Torrey Club **68**: 618–635.

Esau, K. 1942. Vascular differentiation in the vegetative shoot of *Linum.* I. The procambium. Am. Jour. Bot. **29**: 738–746.

Foster, A. S. 1938. Structure and growth of the shoot apex in *Ginkgo biloba.* Bull. Torrey Club **65**: 531–556.

——————. 1939a. Problems of structure, growth and evolution in the shoot apex of seed plants. Bot. Rev. **5**: 454–470.

——————. 1939b. Structure and growth of the shoot apex of *Cycas revoluta.* Am. Jour. Bot. **26**: 372–385.

——————. 1941. Comparative studies on the structure of the shoot apex in seed plants. Bull. Torrey Club **68**: 339–350.

——————. 1943. Zonal structure and growth of the shoot apex in *Microcycas calocoma* (Miq.) A. C. Am. Jour. Bot. **29**: 56–73.

Gifford, E. M. 1943. The structure and development of the shoot apex of *Ephedra altissima.* Bull. Torrey Club **70**: 15–25.

Härtel, K. 1938. Studien an Vegetationspunkten einheimischer Lycopodien. Beitr. Biol. Pfl. **25**: 126–168.

Johnson, M. A. 1939. Structure of the shoot apex in *Zamia.* Bot. Gaz. **101**: 189–203.

Kliem, F. 1937. Vegetationspunkt und Blattanlage bei *Avena sativa.* Beitr. Biol. Pfl. **24**: 281–310.

Korody, E. 1937. Studien am Spross-Vegetationspunkt von *Abies concolor, Picea excelsa* und *Pinus montana.* Beitr. Biol. Pfl. **25**: 23–59.

Korschelt, P. 1884. Zur Frage über das Scheitelwachsthum bei den Phanerogamen. Jahrb. Wiss. Bot. **15**: 642–674.

Pilger, R. 1926. Gymnospermae. In: Engler, A. & Prantl, K. Die Natürlichen Pflanzenfamilien. ed. 2. **13**: 1–447.

Reeve, Roger M. 1942. Structure and growth of the vegetative shoot apex of *Garrya elliptica* Dougl. Am. Jour. Bot. **29**: 697–711.

Rösler, P. 1928. Histologische Studien am Vegetationspunkt von *Triticum vulgare.* Planta **5**: 28–69.

Satina, S. & Blakeslee, A. F. 1941. Periclinal chimeras in *Datura stramonium* in relation to development of leaf and flower. Am. Jour. Bot. **28**: 862–871.

Sharman, B. C. 1940. A periclinal division in the 'dermatogen' at the tip of the maize growing point. Nature **146**: 778–779.

Strasburger, E. 1872. Die Coniferen und die Gnetaceen.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 349–368 JULY, 1943

THE MORPHOLOGY AND ANATOMY OF CALOPOGON PULCHELLUS

MARGERY C. CARLSON[1]

Orchids, particularly the tropical species, have been studied by numerous investigators, especially with regard to the breeding of new varieties, the germination of the seeds, and the relationship to mycorrhizal fungi, but in spite of the importance of their morphology in determining their relationship with other seed plants, much work remains to be done.

Beginning with the investigations of the morphology of orchids by Irmisch (13) in 1853, many pieces of work have treated the subject of the anatomy of the several organs of orchid plants. These investigations are listed in the chronological bibliography presented by Solereder and Meyer (17). The observations were collected and extended by them in their chapter on the Orchidaceae, from which one can obtain specific information about the cell structure, cell contents, and arrangement of cells in leaves, stems, and roots of mature plants of hundreds of species of orchids.

Probably the earliest attempt to treat the anatomy of the monocotyledons comparatively was that of Guillaud (12) in 1878. He presented a brief life history of *Epipactis palustris* Crantz. as representative of the orchids. Some attention was paid to the orchids by de Bary (2) in his "Comparative Anatomy," but perhaps the best known work in this field is that of Arber (1). She summarized the available information on the development and structure of the orchids with a view to showing their relationship to the other monocotyledons. She pointed out the importance of using knowledge of internal structure as well as knowledge of external form in the study of phylogeny, and emphasized the inadequacy of our knowledge of the anatomy of the orchids.

Recently Fuchs and Ziegenspeck (8, 9, 10) made an extensive study of the structure and development of terrestrial orchids native to Europe. Because they were unsuccessful in growing plants from seed, they collected their plants in various stages of development in the field. They described and diagramed the gross anatomy and developmental story, studied cross and longitudinal sections to determine the character and arrangement of the tissues, and traced the entrance and penetration of the mycorrhizal fungi. They studied plants belonging to the following genera: *Orchis*, *Cypripedium*, *Helleborine*, *Limodorum*, *Cephalanthera*, *Listera*, *Neottia*, *Goodyera*,

[1] The author wishes to express her thanks to the Boyce Thompson Institute for Plant Research for the use of its facilities while this work was in progress and for furnishing the photomicrographs.

Liparis, Achroanthus, Malaxis, Corallorhiza, Epipogon, Spiranthes, Coeloglossum, Platanthera, Herminium, Gymnadinea, Nigritella, Neottianthe, and *Ophrys.*

Results of studies on the artificial culturing of orchids may be found in the work of Knudson (14, 15), Curtis (7), and Carlson (5). The recent work of Burgeff (3, 4) summarizes our knowledge of the germination of orchids seeds, the development of seedlings, and the cytology, physiology, and classification of the mycorrhizal fungi and their function in the orchid plants. It gives directions for isolating and identifying the fungi, and for planting seeds and caring for the seedlings, and it contains a good bibliography of these phases of the investigations.

MATERIALS

Calopogon pulchellus (Sw.) R. Br., the grass pink, was chosen for this study because the early stages in its development can be obtained by germinating the seeds and because it has not been studied previously. The species grows in bogs and wet meadows throughout the United States and Canada. Seeds and plants for this study were collected from sphagnum bogs near Sayner, Wisconsin.

The seeds were planted on a nutrient medium in culture bottles, as described by Knudson (14, 15), Curtis (7), and Carlson (5). Seedlings in different stages of development and also parts of older plants collected in the field were fixed in a modified solution of formalin-aceto-alcohol, consisting of 6 parts of 50 per cent alcohol, 3 parts glacial acetic acid and 1 part of formalin. Sections were cut 10 or 12 μ in thickness, mounted in serial order, and stained with safranin and fast green. Great difficulty was encountered in cutting corms whose cells were filled with starch. Fresh corms were sectioned free-hand and the sections kept in serial order on the slides. In most cases the starch was removed with a dilute solution of sulphuric acid and the sections were then preserved on the slide in a 50 per cent solution of glycerine in water.

OBSERVATIONS

The Seed. The seed (fig. 1a) consists of a transparent, loose-fitting seed coat and an ellipsoidal embryo. The seed averages 0.68 mm. in length and 0.20 mm. in width, and the embryo averages 0.27 mm. in length and 0.15 mm. in width (averages from measurements of 60 seeds). The seed coat is a membranous air-filled sac, open at the funicular end where it was broken away from the placenta. It consists of a single layer of elongated, empty cells whose thickened walls give positive tests for lignin and cellulose with the standard methods. The embryo is a mass of undifferentiated parenchymatous cells. The cells in the anterior part (toward the chalazal end of the seed) are small, with dense cytoplasm and centrally placed nuclei, whereas

those of the posterior part are larger and more vacuolated. The embryo is not differentiated into epicotyl, hypocotyl, and cotyledon, but the anterior part of the embryo becomes a bud and might be considered an epicotyl. The much larger posterior portion of the embryo is a food-storage region which might be considered a cotyledon. No primary root is present. Oil globules are found in the dormant embryo, but neither starch nor sugar is present. The walls of the cells of the embryo give a positive test for cellulose. The remains of the integuments and nucellus of the ovule form a brown beak-like cap over the basal, or micropylar, end of the embryo. Filamentous strands of

FIG. 1. Seed and young seedlings of *Calopogon pulchellus* (Sw.) R. Br. a. Seed. b. Germinating seed, embryo enlarged. c. Later stage, apical end of embryo becomes a protocorm. d. Protocorm still larger, seed coat split at chalazal end. e. Seedling with protocorm and bud at apical end, primordium of first leaf evident. f. Older seedling showing protocorm, absorbing hairs, developing bud, primordia of two leaves, seed coat still attached.

cells, probably remaining after the disintegration of the inner cells of the ovule, as in *Cypripedium parviflorum* (6), suspend the embryo in the center of the seed coat, and can be seen attached to the embryo when it is removed from the seed coat.

The Seedling. The seeds germinate soon after being planted in a suitable medium (4). The embryo enlarges and becomes green. At first the seedling retains its oval shape (fig. 1b) because the enlargement is uniform in all dimensions, but in a few weeks the apical end enlarges more rapidly than the basal end, both in length and in width, and the seedling becomes egg-shaped (fig. 1c). It stretches the seed coat laterally, and finally splits it at the chalazal end (fig. 1d).

As growth continues, the differences between the apical and basal ends of the seedling become more marked. The cells of the basal part enlarge greatly, whereas those of the upper part divide and produce a typical promeristem. The oil disappears and reducing sugars and starch appear. Certain cells of the epidermis elongate outward and become absorbing hairs which resemble root hairs. These hairs are produced singly or in small groups, and their length depends on external conditions. The seed coat may remain attached for a time, but is eventually shed. The seedling at this stage of development will be called a protocorm, or first corm (fig. 1e).

A bud now develops from the promeristem and appears as a cone-shaped protrusion. A circular ridge of cells, which arises from the promeristem, is the primordium of the first leaf. A second leaf-primordium arises in the same manner, within and above the first (fig. 1f). A median longitudinal section of a seedling at about this stage of development (fig. 4) shows the bud, with its two concentric tubular leaf-primordia enclosing the promeristem, and its food-storage region still constituting the greater part of the seedling.

When mature, the first or outer leaf is only about 2 or 3 mm. long, and consists of a tubular sheath whose tip is somewhat spread out (fig. 2A). The second leaf becomes longer than the first, and extends through and beyond the opening in the tip of the first. The second leaf also has a tubular sheath whose upper part flattens out into a small blade. The second leaf may be from 5 to 10 mm. long when mature (fig. 2B). During the elongation of the first two leaves, a third leaf-primordium develops from the promeristem directly above the second leaf (fig. 5) and a fourth develops above the third. Each new leaf has a sheath-like base which extends through and beyond the opening in the sheath of the preceding leaf. The tip of the sheath becomes an increasingly longer blade on each succeeding leaf (fig. 2E). Usually only four leaves develop on a seedling. They are arranged alternately in two ranks and are attached close together because the internodes do not elongate. The protocorm, that is, the portion of the seedling below the first leaf, may elongate considerably (fig. 2C, D, E).

The first root of the seedling arises adventitiously either in the upper part of the protocorm or in the bud. Its origin and development will be described later.

By mid-season of the first year, the young plant consists of the protocorm with its absorbing hairs, the shoot with its four concentric leaves in two opposite ranks, and usually, although not always, an adventitious root. The first leaf is chiefly a sheath, but the later ones have linear grass-like blades in addition to their sheaths (fig. 2).

During the later part of the first season, the meristematic tip of the stem stops growing, and a new corm (the second) begins to form by the elongation and enlargement of the parenchymatous cells of the two upper internodes of

the stem (figs. 2C, D, E, 6). This increase in diameter of the stem starts abruptly just above the second node (counting from the base upward) and ends abruptly at the fourth node. The first or lowermost internode may also elongate, but it does not enlarge in diameter. If it elongates, it appears as a stalk of variable length between the protocorm and the new corm, and is ensheathed by the first leaf. If it does not elongate, the first two leaves are close together at the base of the corm, and their sheaths are stretched and sometimes split by the enlargement of the corm. Because the new corm con-

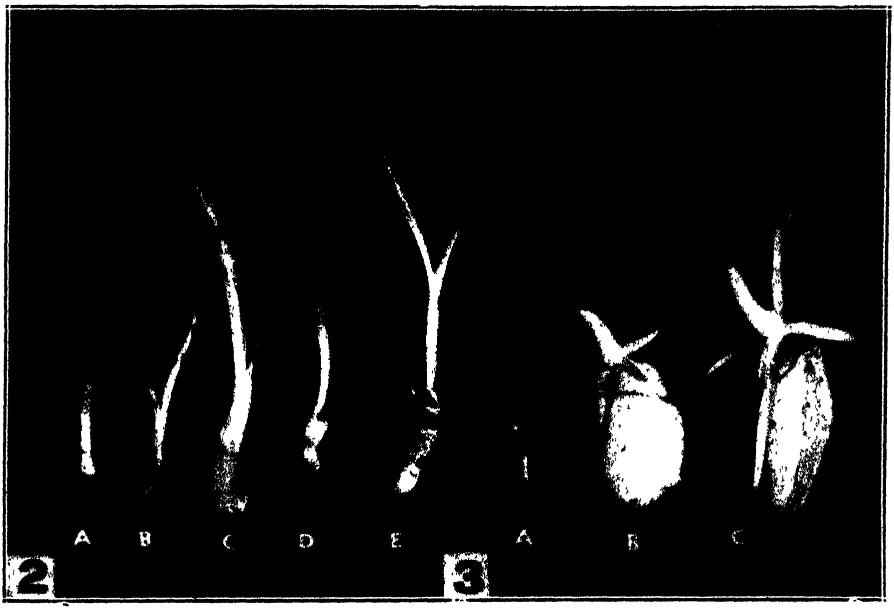


FIG. 2. Plants of first season. A. Young plant with protocorm and young shoot. B. older plant with two leaves expanded. C. Second corm forming at top of protocorm, within sheaths of leaves. D and E. Second corm larger, leaves fully expanded. FIG. 3. Corms of older plants. A. Corm with shoot developing from upper bud, two adventitious roots protruding from base of shoot, lower bud of corm dormant. B. Older corm with developing shoot, whorl of adventitious roots, and dormant lower bud; line across upper part of corm is place of attachment of principal leaf. C. Still older corm with larger shoot and whorl of 7 roots.

sists of the second and third internodes with the intervening third node, the third leaf is attached to the corm. Its base encircles the corm obliquely, usually a little above the middle, and is, of course, much broader than the base of any of the other leaves. Its sheath fits tightly over the top of the corm and encloses the fourth leaf which is attached at the top of the corm. The extreme tip of the corm, which is the meristem of the stem tip, usually dies and appears as a brown spot inside of the sheath of the fourth leaf.

The reserve starch in the cells of the protocorm is gradually digested and passes into the new corm, leaving the protocorm shriveled. The new corm becomes much larger than the protocorm, probably because some of the food manufactured by the leaves and by the corm itself (because its outer layers contain chloroplasts) as well as the excess food from the protocorm passes into the new corm.

The junction between the first and the second corms is seen in figure 6. The first internode has remained short in this case, and the encircling sheaths of the first two leaves are spread apart by the enlarging corm. Because of the abrupt increase in diameter of the second internode, the old and new corms seem to be connected by a narrow neck. Vascular bundles pass from the old to the new corm through this junction, and the cells which surround the bundles in this region become thick-walled and remain free of starch.

As the new corm grows, buds are formed in the axils of the second and third leaves opposite their midribs, but none were found in the axils of the first and fourth leaves. A bud starts as a group of meristematic cells under the epidermis of the corm, and primordia of four leaves develop later from these meristematic cells in acropetal order (fig. 9). The buds develop until they protrude from the surface of the corm, the upper protruding more than the lower. The buds are raised some distance above the attachments of their subtending leaves because the corm enlarges and elongates simultaneously with bud development. A primordium of an adventitious root is formed in each bud. This will be described later.

Toward the end of the first growing season the young plant (fig. 2C, D, E) consists of the small shriveling protocorm which still retains its absorbing hairs; a shoot with four concentric leaves, of which only the upper ones have linear flattened blades; usually an adventitious root arising either from the protocorm or from the base of the shoot; and a second corm filled with starch and enclosed by the sheaths of the leaves.

With the approach of winter, the blades of the leaves succumb to the cold and disintegrate, but their sheaths dry and remain as brown scale-like coverings over the second corm. When all of the food has passed out of the first corm, it gradually disintegrates. The root also dies. Finally all that remains through the winter is the dormant second corm, enclosed by dried sheaths of leaves, with its dormant buds which contain the primordia of leaves and adventitious roots for the next season.

The Plant in the Second Year. With the resumption of growing conditions, the upper lateral bud of the corm begins to grow into a new plant, development, therefore, being sympodial. It breaks through the dried leaf-bases which ensheath the corm. The primordia of the leaves elongate rapidly, but the stem grows rather slowly. The outer leaf becomes a conical sheath

which completely covers the young shoot and gives it the appearance of the seedling shoot of corn. Three or four leaves develop from the bud, of which two have tubular sheaths open at their tops, and the others have linear blades above their sheaths. Each successive leaf is longer than that which precedes it, except the fourth which often does not elongate very much. All of the leaves of the plant of the second year become longer and wider than those of the plant of the first year. The lower bud of the corm, which has the same origin and structure as the upper bud, remains dormant unless the upper bud is removed or injured. The root-tip, which lay dormant in the stem of the bud, elongates and pushes horizontally through the sheath of the first (outermost) leaf of the shoot, and then turns downward.

After the third leaf has completely expanded, another corm (the third) begins to develop in the same manner in which the previous one developed; i.e., by the enlargement and elongation of the second and third internodes of the stem and by the entrance of food from the previous corm. The meristematic tip of the shoot stops growing when the corm begins to form and usually dies. The first (lowermost) internode of the shoot may elongate, but it does not increase in diameter, nor become a part of the new corm. It merely lifts the new corm higher in the medium in which the plant is growing. As in the plant of the first year, buds are differentiated in the axils of the second and third leaves, and a root primordium appears in each bud.

At the end of the second growing season, the plant is larger than, but otherwise similar to, the plant of the first season. It consists of the wrinkled second corm, a lateral shoot with three leaves, a single root, and the third corm enclosed by the sheaths of the leaves. The internode separating the corms may or may not elongate. The tip of the stem dies and appears as a brown spot terminating the corm. Finally all of the plant except the upper corm dies, and the old corm and root disintegrate. The upper corm, enclosed by the dry, brown leaf-bases, lies dormant until the next spring.

Older Plants. The exact age of plants older than two years could not be determined because they were collected in the field and not grown from seeds. However, it was assumed that the larger the corm, the older the plant. A series of increasingly larger corms was studied. The history of their development in succeeding years was found to be much the same as in the first two years.

Each year the plant becomes increasingly larger and more complex (fig. 3A, B, C). Each year a lateral shoot develops sympodially from the upper bud of the dormant corm. If, however, the upper bud is injured, a shoot develops from the lower bud. The shoot produces a short stem, and from three to five concentric leaves. The first two or three leaves are entirely sheathing; the third or fourth bears a lanceolate blade; and the fourth or fifth may or

may not elongate. Each year until the plant is mature, the blade of the principal leaf becomes longer and wider. Each year an increasing number of adventitious roots appears at the base of the shoot. Each year, after the leaves and roots are fully developed, a new corm is formed by the enlargement of the two upper internodes of the stem, and this corm may be lifted upward by the elongation of the first internode of the shoot. A bud is formed in the axil of each of the two leaves of the corm, and new root primordia differentiate in the buds. The tip of the stem dies when the corm is mature. However, when the plant is old enough to bloom, the tip continues to grow and produces an inflorescence which pushes up through the sheath of the inner leaf, and extends beyond its blade. This inflorescence consists of a peduncle and a raceme with from 6 to 12 flowers. It has not yet been determined how old a plant must be before blooming.

Development and Structure of Roots. The embryo has no primary root, hence all the roots of the plant are adventitious. The first root of the seedling arises by rapid nuclear and cell divisions in a small group of parenchymatous cells in the outer cortex of the upper part of the protocorm. The group of meristematic cells enlarges and becomes differentiated into a typical root-tip, and then elongates and extends horizontally outward. The root may stretch the epidermis before breaking it and emerging (fig. 7). The root remains unbranched. Often this root from the protocorm is absent, in which case a primordium (or occasionally two) arises in the bud. It appears as a group of meristematic cells in the outer cortex of the internode between the first and second leaves (fig. 5). This group of meristematic cells becomes a root-tip which elongates, digests its way through the epidermis of the stem and the sheath of the first leaf, and emerges. Sometimes, however, the seedling has no root (fig. 2), and absorption is then entirely accomplished by means of the epidermis and the absorbing hairs of the protocorm.

In each succeeding year, when the upper bud of the corm develops into a shoot, adventitious roots arise at its base (fig. 3). The number of roots per year increases as the plant ages. An early stage in the formation of a root primordium (figs. 9, 12, 32) shows a small group of meristematic cells in the outer part of the stem, just below the attachment of a leaf. This group of meristematic cells becomes dome-shaped, as in figure 9, and may remain dormant in this condition during the winter, or may differentiate into a typical root-tip before dormancy begins. When the bud grows in the spring, the root-tip elongates horizontally and digests its way through the epidermis of the stem and the bases of one or more leaf-sheaths which enclose it (figs. 11, 29–34). The root-tip, or tips, which originate in the lower bud of a corm do not develop into roots if this bud is inhibited in its growth by the growth of the upper bud.

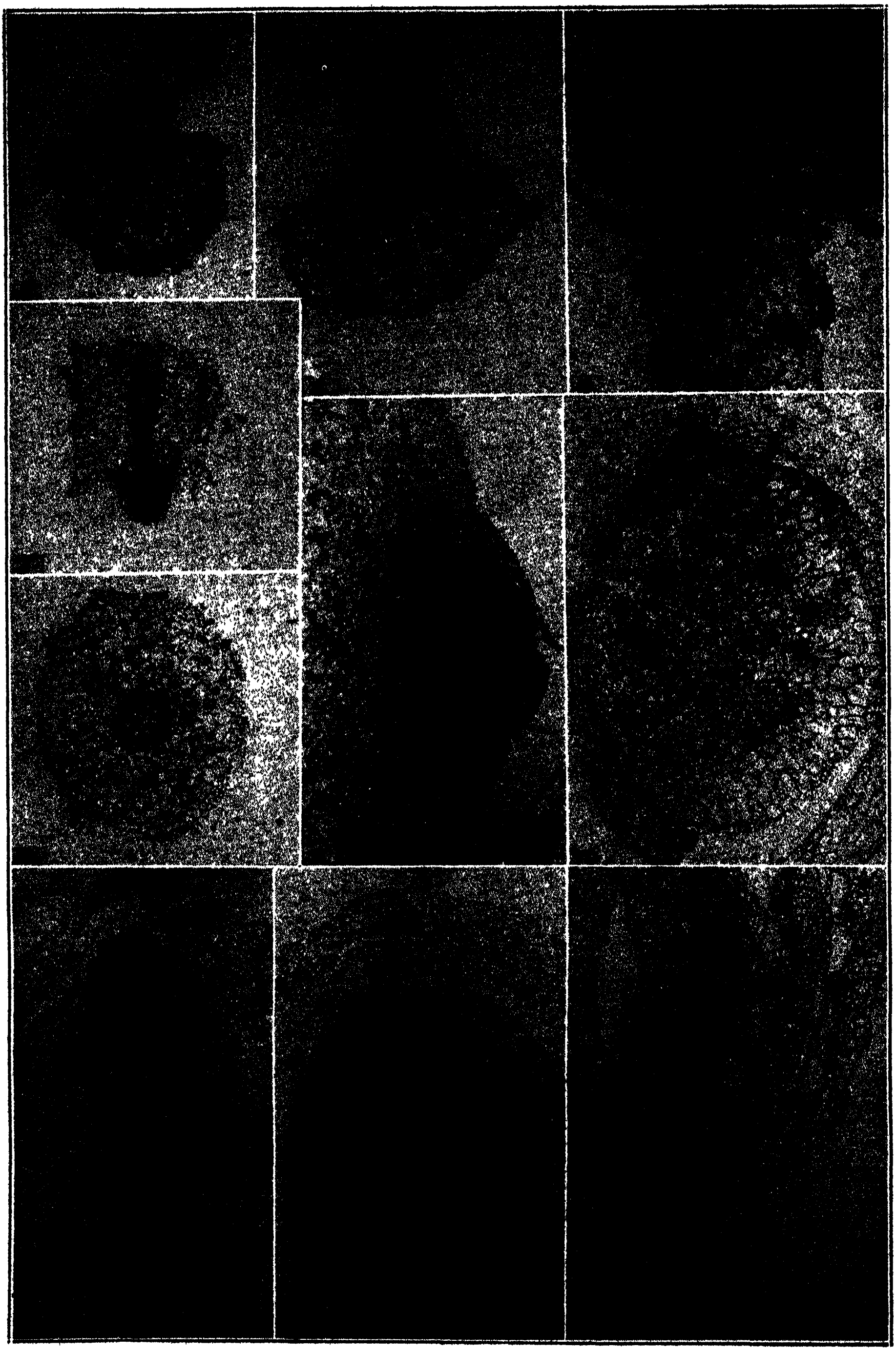
The roots of older plants form whorls in a zone at the base of the lateral shoots (fig. 3). The positions of the ten roots of a medium-sized plant are seen in figures 29–34, where the roots are numbered in the order of their position, beginning with the lowermost. This order is not necessarily the order of their age (for example, the seventh and eighth roots are younger than the ninth), but usually the lower roots are older than the upper ones. In the plant illustrated, the roots seem to be approximately opposite each other in series, that is, the first is opposite the third, the second opposite the fifth, the fourth opposite the sixth, and the seventh opposite the ninth. The eighth, however, is not opposite the tenth. Too few cases have been studied to permit generalizations concerning the regularity of the positions or the order of development of the roots. They extend outward in all directions from the shoot and are unbranched.

A mature root (fig. 8) consists of an epidermis, bearing root-hairs, a parenchymatous cortex, a well-defined endodermis, a stele with radially arranged xylem and phloem and a small pith. The endodermal cells have Casparian strips on their radial walls, and the cells of the pericycle are thin walled opposite the xylem and thick walled opposite the phloem. The exarch xylem and phloem are surrounded by sclerenchymatous cells. The number of alternating strands of xylem and phloem increases from four (tetrarch) in young roots to many (polyarch) in older ones. Hyphae of the mycorrhizal fungus, which entered through the root-hairs, form knots in many of the cells of the cortex.

Structure of Leaves. The three or four leaves of the seedling consist of two or three layers of undifferentiated mesophyll between the epidermal layers (figs. 4, 5). The outer leaf has a single median vein, and each of the others has three parallel veins, a median one and two smaller lateral ones. The cross section of the median vein shows only a few tracheids and sieve tubes, surrounded by a parenchymatous bundle sheath. The lateral veins may show only a single tracheid and one or two phloem cells in cross section.

After the first year, the shoot produces from three to five leaves each year. Only one (usually the third) bears the elongated grass-like blade by which the plant is recognized during the growing season. Its blade (limb) and sheath are separated by a joint, but no ligule is present. The lower leaves are tubular sheaths. Sometimes a smaller leaf with a diminutive blade appears above the principal leaf.

All the leaves become longer, wider, and thicker each year, and the number of veins in each increases. When young, a plant has three veins in each leaf; when older, five; then seven; and when old enough to bloom, it may have from thirty to forty veins. The larger veins enter the leaf from the stem separately, and the smaller veins arise as branches from the larger ones. All the veins are parallel, but small cross-veins connect adjacent veins at



frequent, irregular intervals. All the veins join near or at the pointed tip of the leaf.

The leaves of an individual plant differ somewhat in structure (figs. 12, 13). They are progressively thicker from the lower to the upper. In all leaves the epidermal layers are thinly cutinized, and the mesophyll consists of simple parenchymatous cells, smaller in the outer half of the leaf, and larger in the inner half, but with no differentiation into typical palisade and spongy tissue. Large air spaces appear in the inner mesophyll of the lower leaves. The veins are surrounded by sclerenchymatous bundle sheaths. The larger collateral veins contain both xylem and phloem and the smaller veins may contain only phloem. Smaller strands between the veins may be composed entirely of sclerenchyma. The main veins are progressively larger from the lower to the upper leaf.

Vascular System. The embryo has no vascular tissue, but when the apical bud is formed on the protocorm, a small central provascular strand is differentiated at the base of the bud (fig. 4) and continues upward as the bud develops. This strand becomes a simple protostele (fig. 26), its differentiation beginning at the lower end and proceeding upward. The stele is bounded by an endodermis of large thin-walled cells with conspicuous Casparian strips on their radial walls and by a parenchymatous pericycle of one layer of cells. The xylem consists of a few scalariform tracheids; the phloem

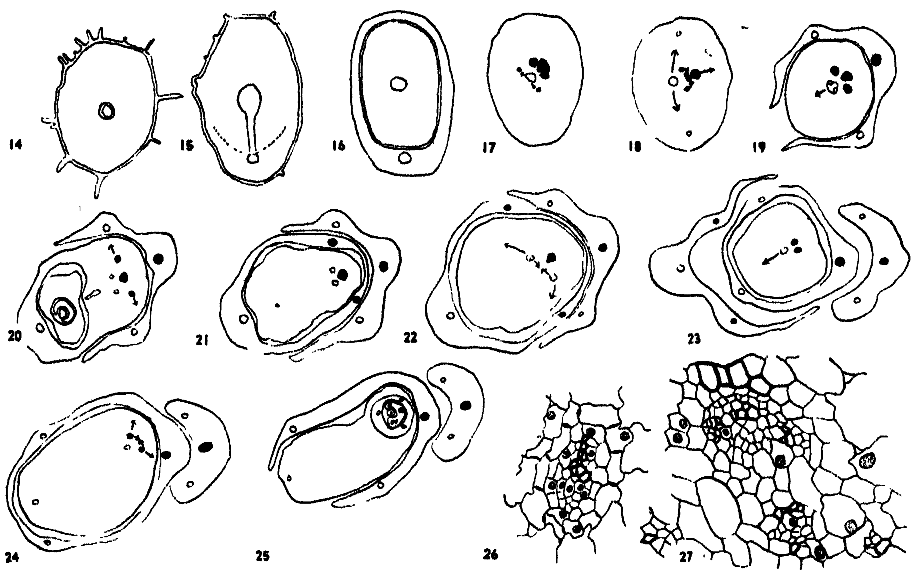
Explanation of figures 4–13.

Photomicrographs, showing structure of plant at different stages of development. Fig. 4. Median longitudinal section of a young seedling (about same age as seedling in figure 1a) showing protocorm with provascular strand, meristem of bud, primordia of two concentric leaves. Fig. 5. Longitudinal section (not median) of a seedling somewhat older than that in figure 4, showing protocorm, second leaf longer than first, primordium of third leaf, and primordium of first adventitious root below the attachment of the second leaf. Fig. 6. Longitudinal section of a seedling (about the same age as the seedlings in figure 2D, E), showing portions of protocorm (below) and second corm (above), second corm with starch, protocorm with none; thick-walled cells above and below narrow junction between 2 corms, sheaths of 2 lower leaves stretched by second corm. Fig. 7. Cross section of protocorm at level of first root, showing root protruding and stretching epidermis; provascular strand between center of root and stele of protocorm. Fig. 8. Cross section of mature root of old plant. Fig. 9. Portion of section of corm of old plant, showing bud with primordia of leaves, provascular strands, and primordium of adventitious root between first and second leaf-primordia; bud covered by corm tissue. Fig. 10. Cross section of base of shoot, just above its separation from corm. Vascular bundles from corm, each with circular strand of phloem, relatively small amount of xylem, and sclerenchymatous bundle-sheath. Fig. 11. Cross section of same shoot between first and second nodes; a, c, d, e, midrib and midrib traces of first, third, fourth and fifth leaves, respectively. Young root digesting way through epidermis of stem and outer leaf, vascular connection of root and stem. Portion of cylinder of sclerenchymatous cells, showing connection with stele of older root. Fig. 12. Cross section of same shoot at third node; letters, as above. Portions of sheaths of three leaves, young bud (upper left), provascular strands extending horizontally toward bud, root primordium (lower right) at base of third leaf, 7 large and 8 small traces to fourth leaf. Fig. 13. Portions of cross sections of three mature leaves.

consists of a few sieve tubes and companion cells. The arrangement of xylem and phloem appears to be monarch.

If a root is formed in the protocorm, a simple protostele is differentiated inward from the center of the root and meets the central stele of the protocorm at a right angle (fig. 7).

The upper part of the vascular system of the seedling consists entirely of leaf traces which make a two-sided pattern in supplying the two ranks of alternate leaves. This vascular system will be described from the base of the seedling upward (figs. 14–25) rather than in the direction of its differen-



FIGS. 14–27. Vascular system of plant of first season. FIGS. 14–25. Series of cross sections from base upward, showing course of vascular bundles. Traces originating from one main bundle in black; those from other main bundle in white. FIG. 14. Through protocorm, with protostele and absorbing hairs. FIG. 15. Trace to first leaf, at a right angle with protostele. FIG. 16. Sheathing first leaf, with one vein; one vascular strand in stem. FIGS. 17–18. First internode; larger of two main bundles (black) separated into three, median becomes median trace of second leaf, laterals each divide into two; other main bundle (white) separated into three. FIG. 19. Base of second corm above second node. Second leaf with three veins. Inner branches of two laterals (black) fused, median (white) divided into three. FIG. 20. Third node, leaf not entirely separated. Midrib of leaf and trace to bud from median of above three (white), two lateral traces (black) to third leaf. FIGS. 21–22. Above third node. Second and third leaves, three veins each; three bundles (1 black, 2 white) continuing upward. FIG. 23. Above fourth node. Larger bundle (black) divided into three, middle becomes median trace to fourth leaf; two smaller bundles (white), each divide into two, inner branches unite, outer become lateral traces to fourth leaf. FIGS. 24–25. Top of second corm. Fused bundle (white) divides into two, one goes to tip of corm and other to bud in axil of fourth leaf; two bundles (black) go to same bud. FIG. 26. Detail of protostele from figure 14. FIG. 27. Detail of bundles from figure 17.

tiation from the tip downward. The central stele of the protocorm "divides" into two unequal bundles. The smaller bundle "passes into" the first leaf (fig. 15), and the larger continues upward for a short distance and then "divides"[2] into two. The larger of these bundles, shaded black in figures 17–25, gives rise to one-half of the vascular system, and the smaller, white in figures 17–25, gives rise to the other half. Each half will be described separately.

The larger of the two main bundles divides into three (fig. 17). The median of these passes into the midrib of the second leaf, and each of the two smaller lateral ones divides again (fig. 18). The two outer of these traces become the lateral veins of the third leaf (fig. 21). The two inner bundles join into a single bundle which continues upward to the fourth node (figs. 19–22) and then divides into three. The median bundle of these three goes to the midrib region of the fourth leaf (fig. 23), and the other two go to the bud in the axil of the fourth leaf.

The course of the bundles on the opposite side of the seedling is similar. The smaller main bundle in the first internode divides into three (fig. 18), the two lateral ones becoming lateral traces to the second leaf, and the central one continuing upward to the second internode, where it again divides into three (fig. 20). The median one of these three divides into two, one of which passes into the midrib of the third leaf and the other of which passes into the bud at the third node (fig. 20). Each of the two lateral bundles divides into two, the outer two becoming the lateral veins of the fourth leaf; the inner two joining and continuing upward to the tip of the seedling (figs. 23–25). Thus the median traces of the second and fourth leaves and the lateral traces of the third form one-half of the vascular system, and the median traces of the first and third and the lateral traces of the second and fourth leaves form the other half of the vascular system. When the new corm is formed by the enlargement of the two upper internodes, the vascular bundles are merely separated by the enlarging cells of the parenchyma and are not changed in their course.

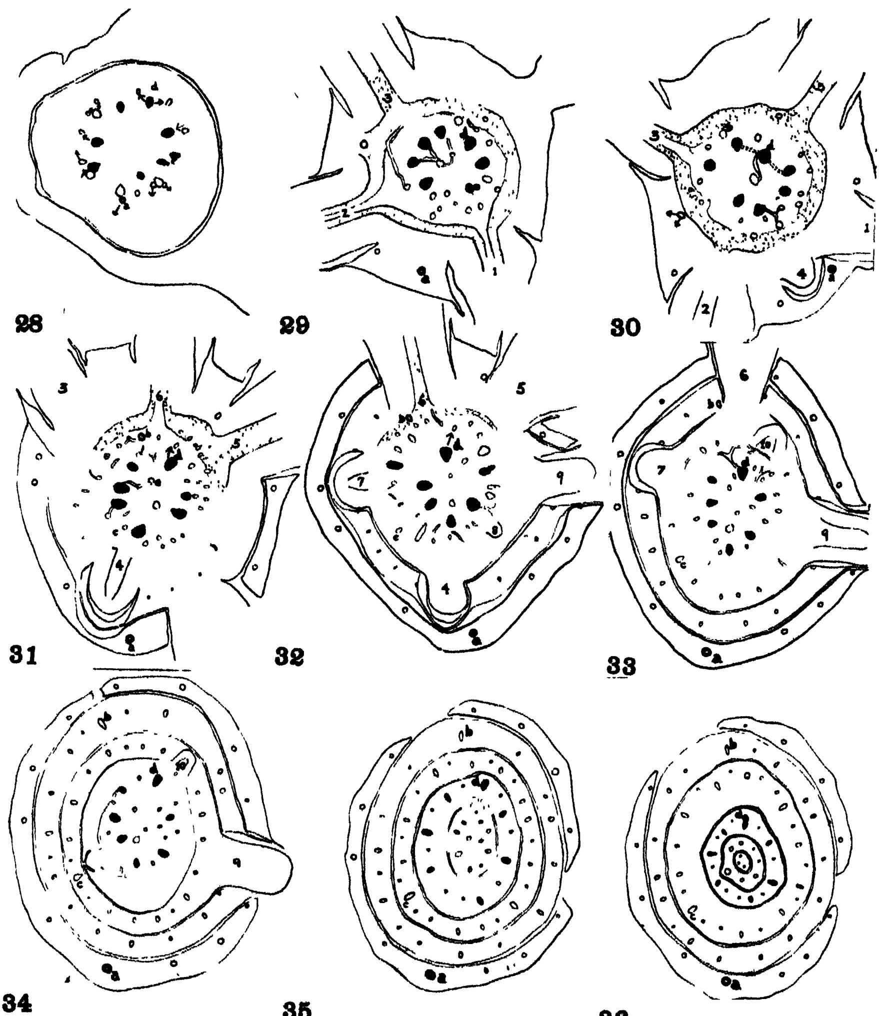
Because the new shoot develops from the upper bud of the corm in each subsequent season, the vascular system of this shoot is differentiated when the bud is developing on the corm, and is joined to the vascular system of the corm very early in the history of the bud. The vascular system matures as the bud grows into the new plant. Each year, as the plant becomes larger, its vascular system increases in number of bundles and complexity of pattern. The number and arrangement of vascular bundles was studied in increasingly older plants. The exact age of these plants was not known, but their

---

2 The stele is said to "divide," to "give off branches" which "enter" other parts, and so forth, much as these expressions may be used of a road all built at one time, not as meaning that such events occur in ontogeny. It is in such a sense that they are used in the rest of this paper; the quotation marks being hereafter omitted.

age was assumed to be related to their size, to the number of veins in the principal leaf, and to the number of adventitious roots at the base of the shoot.

The course of the vascular bundles in an older plant—one with 10 roots and 15 veins in its principal leaf—is illustrated in the series of cross sections in figures 28–36. The upper bud of this plant had begun to develop and



28 29 30 31 32 33 34 35 36

FIGS. 28–36. Vascular system of older plant. Series of cross sections of developing shoot, from base upward. Letters as in figure 11. Principal bundles which enter from corm and extend to fourth leaf in black. Adventitious roots numbered in order of position from base upward. FIG. 28. Base of shoot above separation from corm, as in figure 10. Two irregular rings of vascular bundles, some branching, others fusing (indicated by

the first five roots had emerged at the base of the shoot (as in figure 3B, C) when it was fixed for sectioning. Here, again, the course of the bundles will be described from the base upward. The number of bundles in the base of the shoot varies at different levels because some bundles fuse and others divide. Twenty-one bundles are shown in figure 28. They are placed somewhat irregularly in two rings, the larger bundles in an inner ring and the smaller alternately in an outer ring. Figure 10 shows the character and arrangement of 15 similar bundles in the base of another plant. Each bundle has a circular strand of phloem, a relatively small amount of xylem, and an encircling sclerenchymatous bundle-sheath. Some appear to be either fusing or dividing.

At higher levels in the stem, the vascular system becomes very complex and seems to follow no regular pattern, as it does in the seedlings. The bundles may branch, anastomose, or connect by horizontal cross-bundles. Their course is particularly difficult to follow in the region where the roots emerge (figs. 29–32), because here they pass into and are obscured by a cylinder of cells which become thick-walled. A portion of this cylinder of sclerenchymatous cells is seen in the lower part of figure 11.

The smaller bundles in the base of the shoot supply the first ring of roots and the first leaf. These bundles branch profusely, and several neighboring branches converge and join with the provascular strands of each young root-tip (fig. 11, upper part). As the tissues in the root develop, the sclerenchyma surrounding the bundles to the root becomes continuous with that which surrounds the vascular tissues in the root (fig. 11, lower). The number of bundles which supply a root and the manner in which the collateral bundles of the stem become oriented to form the radially arranged strands of xylem and phloem in the root were not studied.

Other branches of bundles become the traces to the first leaf. These are followed with difficulty because they are obscured by the emergence of the roots below and at the level of departure of the leaf. The midrib and several

arrows). FIGS. 29–30. Below first node. First three roots emerging, cylinder of sclerenchymatous tissue (stippled), vascular bundles branching, anastomosing, and connecting by cross-bundles, traces of first leaf (ringed heavily). FIG. 31. First node. First leaf partly separated from stem, three additional roots, part of ring of traces to second leaf in cortex, two central bundles present. Photomicrograph (reversed) of portion of this section in figure 11. FIG. 32. Second node. Second leaf partly separated from stem, seventh root penetrating base of second leaf, young primordium of eighth root in cortex of stem, ring of traces to third leaf forming. FIG. 33. Second internode. Ring of traces to third leaf, ninth root penetrating first and second leaves, primordium of tenth root in cortex of stem. FIG. 34. Third node. Three sheathing leaves, axillary bud of third leaf, ring of 15 traces to fourth leaf forming, 6 bundles in center of stem continuing upward. Photomicrograph (reversed) of portion of this section in figure 12. FIG. 35. Fourth node below leaf and bud, 7 traces to fifth leaf, 2 bundles continuing upward to stem tip. FIG. 36. Tip of shoot. Five concentric leaves, with 12, 17, 21, 15, and 7 veins, respectively.

other traces, however, can be followed in figures 29 and 30. They simply pass through the cylinder of thick-walled cells, extend obliquely upward across the cortex, and enter the base of the leaf. Of the 12 strands in the first leaf, several are small, consist only of sclerenchymatous cells, and should probably not be called veins. These seem to have no connection with the bundles in the stem.

The seven larger bundles in the base of the shoot (black in figs. 28–36) also give off numerous small branches which become arranged in concentric rings and supply the other leaves and roots. One ring of 17 traces supplies the second leaf and another of 21 supplies the third (figs. 29–34). Some of these are seen in detail on either side of the root in figure 11. The seven main bundles, together with eight smaller alternating branch-bundles, finally enter the base of the fourth leaf (figs. 33–35, 12) which is the principal leaf of the plant. Two central bundles which originate below the first node become the midribs of the fifth and sixth leaves. One of these, together with six additional branch-bundles, supplies the fifth leaf, and the other goes to the tip of the stem.

The courses of the seven main bundles were followed from the corm upward to the base of the fourth leaf in order to discover a possible plan in their branching. No such plan was found. The course of the median trace to the fourth leaf (d in figs. 28–36, 11, 12) will be described. In the base of the stem it gives off two branches, one extending outward from each side (fig. 28). At a higher level, it gives off another branch (fig. 29) which enters the fifth root. Still higher it connects by a cross-bundle with one of the bundles in the center of the stem (fig. 30), and above this it connects by two cross-bundles with the two adjacent main bundles (fig. 30, dotted lines). Continuing upward, it then gives off, toward the outside, two small bundles (figs. 31, 32, arrows) which become leaf traces to the second leaf, and finally another which divides into two (fig. 33), which become traces to the third leaf. It then passes into the midrib region of the fourth leaf without further branching.

A similar study of the vascular systems of many older plants indicated that the larger bundles entering the stem from the corm extend upward, giving off many branches, and become the principal veins of the principal leaf; that usually an odd number of veins enters this leaf; that the number of veins in the sheathing basal leaves is greater than the number in the principal leaf; that the number of veins in the blade of the principal leaf is greater than the number in its sheath because some of the veins in the blade branch; that the branches from these bundles supply the other leaves and roots. The number of strands per leaf may be large; for example, the outer leaf in figure 13 has 51, the second has 58, and the third has 31. The number of principal veins in these leaves is 19, 11, and 9, respectively.

DISCUSSION

The interpretation of the structure of the embryo of orchids presents difficulties. The embryo may be considered simple and undifferentiated (Arber, 1, p. 166), lacking all of the parts of a typical monocotyledonous embryo and consisting of only a food-storage region and a meristematic region. When the seed germinates, the posterior portion of the embryo supplies food to the anterior meristematic region which produces a more or less enlarged and elongated axis with a bud at its apex. The bud develops into a stem with sheathing leaves at its nodes, and might, therefore, be considered a plumule (epicotyl?). But how shall the axis-like part, which lies between the original food-storage region and the insertion of the first leaf, be interpreted? It becomes green because of the formation of chloroplasts in the outer layers of its cortical cells. It may produce absorbing hairs all over its surface. Its central vascular strand is a monarch protostele, surrounded by a well-differentiated endodermis. The first root of the seedling often originates in this part of the seedling. Goebel (11, pp. 1402–3) calls this part of the axis a hypocotyl. It has many of the features of a hypocotyl, but if it is one, must the leaf at the first node be considered a cotyledon, or does the hypocotyl join the epicotyl with no cotyledon at the junction? I have called this part of the axis a protocorm, or first corm, simply because it enlarges in diameter and becomes filled with starch. I have assumed that the hypocotyl is lacking and that the plumule produces the shoot which bears true leaves at its nodes.

There seems to be no question about the fact that a primary root is lacking in the embryo. This absence of a root is not surprising, because the primary roots of many other monocotyledons are lacking or ephemeral. Arber (1) states that the differentiation of a primary root at the suspensor pole of the embryo is prevented by the presence of the endophytic fungus in the cells of this pole. This cannot be true of *Calopogon pulchellus* because no endophytic fungus was present in the embryos nor in seedlings grown in a sterile culture medium. All of the roots of *C. pulchellus* are adventitious, arising in the cortical parenchymatous cells of the protocorm or of the lower nodes of the stem.

Is a cotyledon present in the embryo? Some might interpret the food-storage region of the embryo as a cotyledon; others might assume that the first leaf is a cotyledon; while still others might conclude that a cotyledon is lacking. In this work I have taken the last position.

Growth of *C. pulchellus* is sympodial; that is, the new shoots arise from lateral buds. Sympodial growth is common among the orchids and other monocotyledons. The terminal bud ceases growth and differentiation and usually dies, but the causes of the cessation of growth or death of the termi-

nal bud are not known. Arber (1, pp. 29, 221), reporting work by Bernard, suggests that growth and differentiation slow down or cease when tuberization begins and that tuberization begins when the plant becomes infected with the mycorrhizal fungus. Knudson (14, 15) showed that certain effects of the fungus could be replaced by the addition of certain carbohydrates. Whether or not the cessation of terminal growth and the tuberization of the two upper internodes (with the intervening node) of the stem of *C. pulchellus* are related to infection by a mycorrhizal fungus or to the carbohydrate supply is not known.

The vascular system of the young plant consists of the single vascular bundle in the protocorm and the leaf traces, while that of older plants consists entirely of leaf traces. The single leaf trace of the first leaf "passes" independently across the cortex and joins the bundle in the protocorm at a right angle. The three leaf traces from each of the other leaves fuse in a definite pattern and form two main bundles which join with the bundle in the protocorm. The fact that the trace of the first leaf is entirely separate from those of the later leaves may be a consideration in determining whether or not this leaf is a cotyledon.

Each year after the first, the vascular system of the plant arises in the upper lateral bud of the corm. Provascular strands appear, in the usual manner, during the differentiation of the bud, and those strands to the third leaf-primordium connect with nearby bundles of the corm and become the main vascular bundles of the stem of the new plant. Those provascular strands which become the leaf traces of the first and second leaves, as well as those to the adventitious roots, join the main vascular strands very near the level of the departure of the respective organs. Leaf traces from the fourth leaf (when present) also join to the main vascular strands.

Because each year the older plant consists of only four nodes with the intervening internodes, the pattern of the vascular system is the same, except that the number of bundles increases as the plant gets older. The pattern is different from the palm type (2) and the types in the Cyperaceae and other monocotyledons described by Plowman (16). The main bundles of the plant of *C. pulchellus* "pass" continuously from the corm through two internodes and become the main traces of the third leaf, which is the principal leaf of the mature plant. All other bundles are traces which join the main bundles at the nodes. Anastomoses of bundles are frequent and follow no particular plan.

The plant passes the winter as a corm with two lateral buds. I have used the term "corm" rather than "tuber" because the enlarged stem is short, thick, and axial, and is covered by the dead bases of the ensheathing leaves.

It is similar to a corm of *Crocus*. Each year a new corm is produced by the two upper internodes of the stem and the old corm shrivels and disintegrates.

SUMMARY

1. Seeds of *Calopogon pulchellus* were germinated on a culture medium and the young plants were grown for two years. Older plants were collected in the field. The anatomy of plants from embryo to the age of blooming was studied.

2. The embryo consists of a food-storing region and a meristematic region which develops into a bud. The bud produces a seedling, with a protocorm at its base and four leaves above. The first root is adventitious and may arise from the protocorm or from the first node of the stem. A second corm arises from the two upper internodes of the stem, and the excess food passes from the protocorm to the new corm. All of the plant except the second corm dies at the end of the first growing season.

3. The plant of the second year arises from a bud at the upper node of the corm. It also produces an adventitious root at its base, four or five leaves, and a new corm from the two upper internodes of its stem. The development of the plant is much the same in succeeding years, except that the number of roots becomes greater and the leaves and the new corm become larger each year.

4. The structure of the root, stem and leaves of a mature plant, and the course of the vascular system in seedlings and older plants are described.

Literature Cited

1. **Arber, A.** Monocotyledons. Cambridge University Press. 1925.
2. **Bary, Anton de.** Comparative anatomy of the vegetative organs of the phanerogams and ferns. Transl. by F. O. Bower and D. H. Scott. Oxford, 1884.
3. **Burgeff, H.** Die Wurzelpilze der Orchideen. Gustav Fischer, Jena. 1909.
4. ——————. Samenkeimung der Orchideen. Gustav Fischer, Jena. 1936.
5. **Carlson, Margery C.** The germination of the seed, and development of the seedling of *Calopogon pulchellus* (Sw.) R. Br. Trans. Ill. Acad. **28**: 85–86. 1935.
6. ——————. Formation of the seed of *Cypripedium parviflorum* Salisb. Bot. Gaz. **102**: 295–301. 1940.
7. **Curtis, J. T.** The relation of specificity of orchid mycorrhizal fungi to the problem of symbiosis. Am. Jour. Bot. **26**: 390–399. 1939.
8. **Fuchs, A. & Ziegenspeck, H.** Bau und Form der Wurzeln der einheimischen Orchideen in Hinblick auf ihre Aufgaben. Bot. Archiv. **12**: 290–397. 1925.
9. ——————. Die Dactylorchisgruppe der Ophrydineen. Bot. Archiv. **19**: 163–274. 1927.
10. ——————. Entwicklungsgeschichte der Achsen der einheimischen Orchideen und ihre Physiologie und Biologie. Bot. Archiv. **14**: 165–260. 1926; **16**: 360–413. 1926; **18**: 378–475. 1927; **20**: 275–422. 1927.
11. **Goebel, K.** Organographie der Pflanzen 3. Jena. 1933.

12. **Guillaud, A.** Recherches sur l'anatomie comparée et le développement des tissus de la tige dans les Monocotylédones. Ann. Sci. Nat. VI. **5**: 5–176. 1878.
13. **Irmisch, J. F. T.** Beiträge zur Biologie und Morphologie der Orchideen. Leipzig. 1853.
14. **Knudson, L.** Nonsymbiotic germination of orchid seeds. Bot. Gaz. **73**: 1–25. 1922.
15. ————. Further observations on nonsymbiotic germination of orchid seeds. Bot. Gaz. **77**: 212–219. 1924.
16. **Plowman A. B.** The comparative anatomy and phylogeny of the Cyperaceae. Ann. Bot. **20**: 1–33. 1906.
17. **Solereder, H. & Meyer, F. J.** Systematische Anatomie der Monokotyledonen **6**: 92–242. 1930.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 4, pp. 369–371 JULY, 1943

A FURTHER NOTE ON THE PRODUCTION OF THIAMINE BY ACTINOMYCES

J. ARTHUR HERRICK AND CONST. J. ALEXOPOULOS[1]

In a previous paper in which the writers reported the results of studies on antibiosis between some species of *Actinomyces* and certain fungi (1), it was suggested that certain results "may very well be an indication of the presence of growth stimulating substances secreted in the agar" by the actinomycetes employed in those experiments. In a subsequent paper (2) the writers reported the production of thiamine or its precursors by *Actinomyces viridochromogenus*. In the meantime Mackinnon reported the production of thiamine by *A. albus* (3).

In view of the above, it appeared desirable to test a number of different species of *Actinomyces* to discover if the production of thiamine is widespread in this genus.

EXPERIMENTAL STUDIES

A suitable number of 200-cc. Erlenmeyer flasks, each containing 25 cc. of a liquid medium, prepared according to the formula and procedure previously reported (2), were sterilized by autoclaving at 17 lbs. pressure for 15 minutes. Ten flasks were then inoculated with a heavy spore suspension of each of 24 actinomycetes,[2] respectively. A suitable number of flasks were retained for use as controls.

Nine days after inoculation[3] the actinomycete mycelium was removed by filtration through filter paper, the filtrates restored to their original volumes with distilled water, and their acidities adjusted to pH 5.4. The 250 cc. of each filtrate were divided into 50-cc. portions and returned to five of the original flasks. The sterile control medium was treated in a similar fashion. The filtrates were now sterilized at 17 lbs. pressure for 20 minutes. In order to destroy a thermolabile inhibitor known to be present in filtrates of *A. gougeroti* cultures, these filtrates were immediately reautoclaved at 17 lbs. pressure for another 20 minutes. On the following day all flasks were inoculated with 4-mm. discs cut from young cultures of *Phycomyces blakesleeanus* growing on cornmeal agar in Petri dishes.

[1] The writers wish to express their appreciation to Dr. H. A. Cunningham, Chairman, Department of Biology, Kent State University, for his encouragement and cooperation in providing research facilities.

[2] The writers are grateful to Dr. Selman A. Waksman for supplying 14 of the 24 cultures employed in these experiments.

[3] *A. gougeroti* was permitted to grow 17 days because of its very slow growth rate. *Proa. polychromogenes* and *Micromonospora* failed to grow satisfactorily in the medium used and were discarded after several weeks.

Thirteen days after inoculation the *Phycomyces* mycelia were removed from the filtrates by filtration through filter papers, dried at 100° C, and the dry weights determined. Because of a few contaminations only four of each set of flasks were filtered. The essential data are presented in the accompanying table (table 1).

TABLE 1. *Dry weights of Phycomyces blakesleeanus mycelium produced in 13 days on culture filtrates of various actinomycetes*

Species	Dry weight, in mg., of mycelium from four flasks	Description of the *Phycomyces* mycelium
A. albidoflavus	287	Complete coverage of surface. Heavy sporangiophore production.
A. albosporeus	154	Complete coverage of surface. Medium sporangiophore production.
A. albus	206	Most of surface covered. Medium sporangiophore production.
A. annulatus	166	One-half of surface covered. Medium sporangiophore production.
A. aureus	184	One-half of surface covered. Medium sporangiophore production.
A. bobili	468	Complete coverage of surface. Very heavy sporangiophore production.
A. californicus	111	Complete coverage of surface. No sporangiophores.
A. cellulosae	170	One-half of surface covered. Medium sporangiophore production.
A. fimicarius	131	One-third of surface covered. Medium sporangiophore production.
A. flavovirens	367	Surface completely covered. Heavy sporangiophore production.
A. flavus	118	Little surface growth. Very few sporangiophores.
A. fradii	511	Complete coverage of surface. Very heavy sporangiophore production.
A. gougeroti	442	Complete coverage of surface. Heavy sporangiophore production.
A. halstedii	133	One-half of surface covered. Medium sporangiophore production.
A. madurae	106	One-half of surface covered. Light sporangiophore production.
A. purpeochromogenus	111	One-half of surface covered. Light sporangiophore production.
A. reticuli	256	One-half of surface covered. Heavy sporangiophore production.
A. scabies	340	Complete coverage of surface. Heavy sporangiophore production.
A. violaceous-ruber	228	Three-fourths of surface covered. Medium sporangiophore production.
A. viridochromogenus	191	One-half of surface covered. Medium sporangiophore production.
Proa. asteroides	132	One-half of surface covered. Medium sporangiophore production.
Proa. salmonicolor	92	One-half of surface covered. Very few sporangiophores.
Control	17	Small, completely submerged mycelia. No sporangiophores.

DISCUSSION AND CONCLUSIONS

The growth of *Phycomyces blakesleeanus* as a test for thiamine has been previously discussed (2). A comparison of the growth of *P. blakesleeanus* on the filtrates of the 22 actinomycetes employed in these experiments with that on the control medium is offered as convincing evidence that all of the actinomycetes investigated are able to produce detectable amounts of thiamine, or its precursors, in culture.

Although the species investigated constitute only about one-fifth or less of the total number of actinomycetes known, the fact that all of them gave positive results would seem to indicate that the production of thiamine is very widespread in the genus *Actinomyces*.

SUMMARY

Twenty-two actinomycetes were grown on a thiamine-free liquid medium. The cultures were filtered, the filtrates acidified and autoclaved. All of the 22 filtrates were found to support a considerable growth of *Phycomyces blakesleeanus*. It is therefore concluded that all of the 22 actinomycetes investigated produce thiamine or its intermediates or precursors in culture.

Department of Biology, Kent State University
Kent, Ohio

Literature Cited

1. **Alexopoulos, Const. J. & Herrick, J. Arthur.** 1942. Studies in antibiosis between bacteria and fungi—III. Inhibitory action of some actinomycetes on various species of fungi in culture. Bull. Torrey Club **69**: 257–261.
2. **Herrick, J. Arthur & Alexopoulos, Const. J.** 1942. Thiamine production by *Actinomyces viridochromogenus*. Bull. Torrey Club **69**: 569–572.
3. **Mackinnon, Juan E.** 1942. The effect of *Actinomyces albus* and of thiamin on the growth of *Trichophyton discoides*. Bull. Torrey Club **69**: 21–26.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 372–377 JULY, 1943

VITAMIN DEFICIENCIES OF FIFTY YEASTS AND MOLDS

PAUL R. BURKHOLDER AND DOROTHY MOYER

This paper is a report of studies made on the growth factor requirements of thirty-three strains of yeasts representing twenty-four species, and seventeen strains of molds belonging in thirteen species. Since the vitamin requirements of microorganisms have been extensively reviewed in the recent literature, discussion of various aspects of the subject will not be given here. Our knowledge concerning vitamin deficiencies of the filamentous fungi has been well summarized by Robbins and Kavanagh (1). References to important literature dealing with the vitamin relations of yeasts may be found in a paper by the senior author (2).

Cultures of *Fomes annosus* and *Lenzites betulina* were made available through the kindness of Dr. Ross W. Davidson, Division of Forest Pathology, Bureau of Plant Industry, Washington, D. C. Dr. Alma D. Waterman, Division of Forest Pathology, Bureau of Plant Industry, New Haven, Conn., supplied cultures of *Cytospora* sp. and *Coryne sarcoides*. The species of *Trichophyton, Hormodendron, Phialophora,* and *Sporotrichon* were obtained from Dr. C. W. Emmons, National Institute of Health, Bethesda, Md. The yeast cultures were supplied by Drs. L. J. Wickerham and Kenneth B. Raper, from the Culture Collection of the Northern Regional Research Laboratory, Bureau of Agricultural Chemistry and Engineering, Agricultural Research Administration, U. S. Department of Agriculture, Peoria, Ill. Stock cultures of these microorganisms were carried on yeast-peptone-dextrose agar.

The methods employed in this study were essentially the same as those which have been reported earlier (2). The basal medium employed for cultivation of the molds and yeasts contained the following compounds in each liter of solution: dextrose C.P., 20 gm.; recrystallized asparagine, 2.0 gm.; KH_2PO_4, 1.5 gm.; $MgSO_4 \cdot 7H_2O$, 0.5 gm.; $CaCl_2 \cdot 2H_2O$, 0.33 gm.; $(NH_4)_2SO_4$, 2.0 gm.; and KI, 0.1 mg. Trace elements were added to this medium in p.p.m. as follows: B, 0.01; Mn, 0.01; Zn, 0.07; Cu, 0.01; Mo, 0.01; and Fe, 0.05. Vitamin supplements were added singly or in combination in micrograms per liter of medium as follows: thiamine hydrochloride, 200; pyridoxine hydrochloride, 200; nicotinic acid, 200; biotin methyl ester, 2.0; calcium pantothenate, 200; and inositol, 10,000. Riboflavin was generally omitted from consideration inasmuch as earlier work indicated that yeasts and molds are not commonly deficient for this vitamin.[1] The dosages of

[1] In the series of cultures set up for several human pathogens (figure 1), riboflavin (200 micrograms per liter) was included in the medium.

TABLE 1. *Growth of yeasts in a chemically defined medium with varied supplements of vitamins and liver concentrate. The values represent turbidity units of cultures grown for 72 hours at 25° C.*

Organisms	−Six vitamins	−Biotin	−Pyridoxine	−Pantothenic acid	−Nicotinic acid	−Inositol	−Thiamine	+Six vitamins	+Six vitamins +liver
Candida albicans 416	14	10	148	179	155	139	74	156	210
C. albicans 430	8	8	174	194	190	165	130	205	187
C. albicans 461	6	10	187	192	184	147	156	176	201
C. albicans 462	4	5	224	241	234	202	124	235	281
C. albicans 467	7	0	204	200	192	193	119	190	243
C. albicans 475	0	0	0	0	0	0	0	0	181
C. chalmersi 982	0	4	312	322	322	329	289	262	244
C. chevalieri 309	265	336	391	349	329	340	379	316	623
C. deformans 321	35	290	327	304	314	290	26	340	247
C. flareri 245	0	4	121	113	113	99	98	106	95
C. mycotoruloidea 527	0	1	144	156	148	141	61	149	170
C. parakrusei 316	0	0	162	167	157	149	157	144	182
C. stellatoidea 523	27	29	185	201	189	179	86	195	206
C. stellatoidea 524	0	0	59	63	62	61	54	59	81
C. stellatoidea 525	10	28	191	205	194	190	77	195	220
C. stellatoidea 526	25	36	194	195	193	195	92	195	245
C. zeylanoides 347	0	0	160	148	72	152	147	134	65
Chalara mycoderma 709	3	382	322	375	360	355	8	357	415
Hansenula suaveolens 838	184	174	217	203	227	180	223	172	422
Monilia albicans 414	14	16	138	168	166	151	93	156	169
M. metalondinensis 82	12	23	161	191	203	166	206	189	205
M. metalondinensis 539	12	18	188	170	174	180	121	160	211
Mycoderma lafarii 936	0	36	247	307	222	249	89	211	265
M. vini 939	0	0	0	0	0	0	0	0	124
Pichia alcoholophila 373 (after 9 days)	0	0	820	795	770	820	795	720	790

TABLE 1.—(*Continued*)

Organisms	−Six vitamins	−Biotin	−Pyridoxine	−Pantothenic acid	−Nicotinic acid	−Inositol	−Thiamine	+Six vitamins	+Six vitamins +liver
P. belgica 952	0	3	0	113	110	59	14	109	132
P. Dombrowskii 119	19	233	256	237	204	223	9	244	290
Saccharomyces bayanus 966	26	96	316	161	372	44	257	290	397
S. validus 972	0	0	104	76	89	62	0	117	67
Schizosaccharomyces pombe 9	4	1	107	6	1	4	114	72	193
Torulopsis dattila 171	15	157	174	178	182	184	0	153	88
T. molischiana 218	4	1	174	133	131	156	129	146	199
T. sphaerica 169	0	0	229	90	0	234	193	214	215

biotin and inositol were increased 10 fold over those employed in earlier work (2).

Nine kinds of medium were prepared for testing the growth-factor requirements of each fungus as follows: no addition of vitamins, addition of six vitamins, addition of six vitamins plus Wilson's liver concentrate (or peptone for some molds) 0.5 gm. per liter, and single omissions of each of the six vitamins (table 1). The yeasts were cultivated in liquid media. For the molds, gel-substrates were obtained by addition of 1.5 per cent purified agar to the liquid media. The agar was purified by prolonged extraction of 1 pound of agar shreds in 12 liters of 5 per cent aqueous pyridine. The leached agar was then washed twice with several liters of ethyl alcohol, and finally boiled in 10 liters of alcohol for 12 hours. After filtering in a Büchner funnel, the material was dried in large crystallizing dishes at 60° C. Essentially this same method has been employed by Robbins and Ma (3) for cleaning agar to be used in vitamin studies.

In a few experiments, silica gel was employed as a semi-solid substrate. This part of the work was performed in our laboratory by Mr. E. H. Tryon, who found certain deficiencies in *Cytospora* sp., *Fomes annosus*, and *Coryne sarcoides* with this method. The technique has been discussed recently in connection with cultivation of algae (4) and would seem to offer distinct advantages for cultivation of fungi in defined media.

All the media were adjusted to about pH 5.0 and sterilization was effected in an autoclave operated at fifteen pounds pressure for fifteen minutes. Yeast

inoculum was prepared by transferring a small amount of stock culture into 5 ml. of sterile basal medium free of all vitamins. After thorough mixing to obtain a uniform suspension of organisms, a loopful 4 mm. in diameter was used to inoculate each culture tube containing 5 ml. of one of the designated kinds of media. Duplicate sets of media were employed for each kind of fungus. Growth of yeasts was allowed to proceed for 72 hours at approximately 25° C. Growth was estimated turbidimetrically with a Klett photoelectric colorimeter.

The media for cultivation of molds were inoculated with very small amounts of mycelium or with spores transferred on a platinum wire from stock cultures grown on nutrient agar. The growth period varied from three to six weeks, depending upon the rate of development of the mold. Subcultures were made in sets of deficient media to check further upon vitamin requirements and to reduce the amounts of vitamins which may have been carried over with the inoculum. Growth of the molds was observed by direct examination.

A summary of the growth responses of thirty-three strains of yeasts is presented in table 1. The code number under each species name in the table refers to the number in the culture collection from which the yeasts were derived.

Five strains of *Candida albicans* appeared to be completely deficient for biotin, and partially deficient for thiamine. These strains were isolated originally from poultry or from human hosts. The strain 475 of *C. albicans* isolated from man appears to possess deficiency for some unidentified factor. Fair growth occurred only in the medium containing liver concentrate. The other species of *Candida*, with the apparent exception of *C. chevalieri*, were also deficient for biotin. Several of these showed partial deficiencies for thiamine, and *C. zeylanoides* gave indication of partial niacin deficiency.

In the majority of yeasts biotin is a required growth factor. Next to biotin, vitamin B_1 deficiency appears most frequently. *Pichia belgica* was found to require biotin, pyridoxine, and thiamine; its growth was improved somewhat by addition of inositol. *Saccharomyces bayanus* required some accessory biotin and inositol for maximum growth. *Schizosaccharomyces pombe* grew poorly with single omissions of biotin, pantothenic acid, nicotinic acid, and inositol. *Torulopsis sphaerica* failed to grow in the absence of biotin or niacin and also showed partial deficiency for pantothenic acid.

Candida deformans, Chalara mycoderma, and *Pichia Dombrowskii* appear to be deficient for thiamine but not for biotin. *Candida chevalieri* and *Hansenula suaveolens* showed no deficiency for any of the six vitamins, though much better growth of these species was obtained with liver supplement added to medium containing the six vitamins. *Mycoderma vini* grew in medium containing liver concentrate but not in the synthetic media.

The essential growth factor requirements of seventeen fungi are shown in table 2. It appears from the results of our work and that of others that

TABLE 2. *Vitamin requirements of molds grown in synthetic medium containing purified agar or silica gel and varied supplements of six vitamins, etc.*

Species	Vitamin requirements	Growth in liver or peptone
Hormodendron pedrosoi	Deficient for thiamine	Somewhat stimulated
Phialophora verrucosa	Deficient for thiamine	....
Sporotrichon schencki	Deficient for thiamine	Not stimulated
Trichophyton acuminatum	Partially deficient for thiamine	Not stimulated
T. faviforme	Deficient for thiamine and inositol	Stimulated
T. mentagrophytes 514	No deficiency observed	Stimulated
T. mentagrophytes 517	No deficiency observed	Not stimulated
T. mentagrophytes 598	No deficiency observed	Not stimulated
T. mentagrophytes 599	No deficiency observed	Not stimulated
T. mentagrophytes 607	No deficiency observed	Not stimulated
T. rubrum	No deficiency observed	Somewhat stimulated
T. sulphureum	Deficient for thiamine	Not stimulated
T. violaceum	Deficient for thiamine	Greatly stimulated
*Fomes annosus**	Deficient for thiamine	....
*Coryne sarcoides**	Deficient for thiamine and biotin	....
*Cytospora sp.**	Deficient for thiamine	
Lenzites betulina	Deficient for thiamine	

* Cultivated by E. H. Tryon in nutrient silica gel.

the various species of *Trichophyton* differ in their vitamin requirements. The five strains of *T. mentagrophytes* and *T. rubrum* seem to be able to grow well without the addition of any vitamins. Four other species of *Trichophyton* require thiamine, and *T. faviforme* appeared to be deficient for both thiamine and inositol. Robbins, Mackinnon and Ma (5) have recently found *T. discoides* to be deficient for thiamine, inositol, and pyridoxine. As indicated in table 2, the species of fungi which live in wood, *Cytospora* sp., *Fomes annosus*, and *Lenzites betulina* are deficient for thiamine, while *Coryne sarcoides* requires both thiamine and biotin.

SUMMARY

Vitamin requirements of thirty-three yeasts and seventeen molds, including some important pathogens in both groups, were studied in chemically defined media. Biotin and thiamine deficiencies occurred most commonly.

Deficiencies for pyridoxine, pantothenic acid, inositol, and nicotinic acid were found in several yeasts.

OSBORN BOTANICAL LABORATORY, YALE UNIVERSITY
NEW HAVEN, CONNECTICUT

Literature Cited

1. **Robbins, W. J. & Kavanagh, Virgene.** 1942. Vitamin deficiencies of the filamentous fungi. Bot. Rev. **8**: 411–471.
2. **Burkholder, Paul R.** 1943. Vitamin deficiencies in yeasts. Am. Jour. Bot. **30**: 206–211.
3. **Robbins, W. J. & Ma, Roberta.** 1941. Biotin and the growth of *Fusarium avenaceum*. Bull. Torrey Club **68**: 446–462.
4. **Bold, H. C.** 1942. The cultivation of algae. Bot. Rev. **8**: 69–138.
5. **Robbins, W. J., Mackinnon, J. E. & Ma, Roberta.** 1942. Vitamin deficiencies of *Trichophyton discoides*. Bull. Torrey Club **69**: 509–521.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 378–385 JULY, 1943

INFLUENCE OF TEMPERATURE ON THE INFECTION OF WHEAT BY THE POWDERY MILDEW ERYSIPHE GRAMINIS TRITICI[1]

ROBERTSON PRATT

Discovery and recognition of physiologically specialized forms in the powdery mildews (Neger 1902, Marchal 1902) similar to those then recognized in the rusts and smuts initiated an avid search for more examples of such specialization in this group of obligate ectoparasites. Consequently, papers describing new species or races or extending our knowledge of the host range of these fungi are numerous, while there is a relative dearth of literature concerning other phases of their physiology. The purpose of this investigation was to study quantitatively the effects of temperature, daily period of illumination, and of humidity upon the infection of wheat, *Triticum vulgare,* by the powdery mildew, *Erysiphe graminis tritici.* The present paper is concerned with the effects of temperature.

METHODS

Hanging drop cultures were employed for studies involving the fungus alone. For experiments involving mildew cultures on the host plant under controlled conditions, a thermostatic chamber (Trelease 1925) was employed. Uniform light was provided by a 1000-watt clear Mazda-C electric light lamp and a reflector. To exclude extraneous daylight the light assembly was surrounded by a truncated pyramid of galvanized iron that rested on the top of the incubation chamber. Between the lamp and the glass roof of the chamber was a water screen 25 mm. deep flowing at a rate of approximately 3.2 liters per hour. To insure uniform quality and quantity of radiation, bulbs were discarded after 500 hours of service. Tests showed that mildew response and development were, as far as could be determined, identical throughout this period.

Stock cultures of the mildew were maintained in the greenhouse at 16°–21° C, and experimental plants were inoculated in the manner described by Trelease and Trelease (1928). Experimental plants were grown in mildew-free chambers or under bell jars, and all reasonable precautions were taken to avoid accidental inoculation. At the beginning of each experiment one-half of the plants were inoculated. The remainder were left in a mildew-free chamber in which conditions favorable for mildew development were maintained. If no infection appeared among the control plants within

[1] The work reported in this paper was done in the laboratory of Plant Physiology at Columbia University between 1931 and 1935.

five days, it was considered as reasonably certain that the whole set of plants was mildew-free at the start of the experiment. At the temperature used (16°–21° C), mildew becomes abundant on an infected plant in from two-and-one-half to three-and-one-half days. These plants were then inoculated and used for stock cultures of the fungus. All experimental plants were inoculated at about the same time of day (5:00–6:00 p.m.), so that the photosynthetic and metabolic products within the plants would be as nearly uniform as possible at the time of inoculation in the different experimental sets. Yarwood (1934) has shown that clover leaves removed in the evening are more susceptible to *Erysiphe* than those removed in the morning. Detailed methods and deviations from this general mode of procedure are noted under the experiments concerned.

A virulent strain of mildew which had been maintained in the greenhouse for several years was used. It was not deemed necessary to make a single-spore isolation of the mildews, since very consistent and reproducible results were obtained in all experiments, indicating that if two or more strains of the fungus were present they were equally and similarly sensitive to the experimental conditions imposed upon them. In all experiments, Marquis, a Spring variety of wheat was used as the host. Plants were grown in ordinary loam in four-inch clay pots, about 50 plants in a pot, and were inoculated when the first leaf was fully expanded.

RESULTS

Table 1 and figure 1 show the effect of temperature upon mildew development on wheat plants exposed to twelve hours illumination daily. In all temperature experiments eight pots of plants (about 400 seedlings) were used and each experiment was duplicated. Thus the averages are for 16 sets of plants. High humidity was provided by hanging water-soaked towels around the inside of the incubation chamber. The data in table 1 indicate that the optimum temperature for mildew infection on wheat under the conditions of these experiments is about 20° C. From −2° to 15° C the rate of mildew growth increased rapidly and the effect of temperature on the relative rates of early and late stages of development was about the same (column 5), although the maximum virulence of infection at −2° C was somewhat less than at higher temperatures (column 6). At the optimum temperature (20° C) the processes concerned with maturation and the formation of conidia proceeded relatively about twice as rapidly as at the lower temperatures (column 5). A slight further rise in temperature, however, while not appreciably altering the rate of early growth (column 2) exerted a relatively pronounced effect on the stages of development concerned with vegetative maturation (column 5). At 30° C no macroscopic indications of infection were found.

TABLE 1. *Effect of temperature upon incubation period (time required for mildew to appear) and maturation period (time required for development of conidia minus incubation period)*

(1) Temp.	(2) Average incubation period[a]	(3) Average time for appearance of conidia	(4) Average maturation period[b]	(5) Maturation Period / Incubation "	(6) Virulence of infection (approximate)
– 2°C	17.5 days	28.25 days	10.75 days	0.614	+++
+ 5°C	9.75 "	16.00 "	6.25 "	0.642	+++++
10°C	6.25 "	10.00 "	3.75 "	0.600	+++++
15°C	3.25 "	5.25 "	2.00 "	0.615	+++++
20°C	2.50 "	3.25 "	0.75 "	0.300	+++++
25°C	2.50 "	3.75 "	1.25 "	0.500	+++++
30°C	.....	.....	.	.....	.....

[a] Time elapsed between inoculation of the plants and the first macroscopic signs of infection.

[b] Time required for appearance of first conidia minus incubation period.

Compared with many saprophytic and parasitic fungi, *Erysiphe* appears to have a very low maximum temperature for infection, although Maneval (1922) reported that for twenty species of rusts the maximum temperature for germination of teliospores is less than 30° C. High temperature might prevent infection by a direct deleterious effect upon the fungus either before, during, or after germination of the conidia or by causing changes in the metabolic products or processes of the host that render it unsuitable for supporting the parasite. These possibilities were examined.

Large numbers of conidia were used to determine the effect of temperature upon spore germination in tap water. Hanging drops containing from two to three hundred spores each were kept in darkness at the different temperatures and after twenty-four hours the spores were killed by placing a little formalin in the bottom of the chambers. The total number of spores and the number of germinated spores were then recorded. The data obtained are presented in figure 2, which shows that maximum germination occurred from 15° to 20° C. Either side of that range, germination fell off abruptly. At 35° C there was no germination at all in twenty-four hours, and the spores lacked their natural clear hyaline appearance. Instead, the contents appeared granular and coagulated. The effect of temperature upon spore germination will be referred to below. It suffices here to note that failure to obtain infection of wheat at 30° C was not due to failure of spores to germinate, since germination at that temperature was of the same order of magnitude as at – 2° C, where good infection occurred.

Wheat plants grown from seed at 30° C until the first leaf was fully expanded were inoculated, and at regular intervals two pots of the inoculated plants were transferred to a chamber at 20° C and the remainder were left at 30° C. Minute white patches of mycelium appeared in two and a half days and numerous conidiophores appeared a day later on the plants at 20° C,

but no signs of mildew appeared on those at 30° C even after one week. Microscopic investigation of these leaves revealed no stages of mildew development beyond the production of germ tubes from thirty to forty microns in length. No penetration of the host tissue by the fungus could be found. It may be concluded from these experiments that exposure of wheat seedlings to a temperature of 30° C for the first five days of growth does not produce any change which seriously impairs their normal capacity for supporting mildew

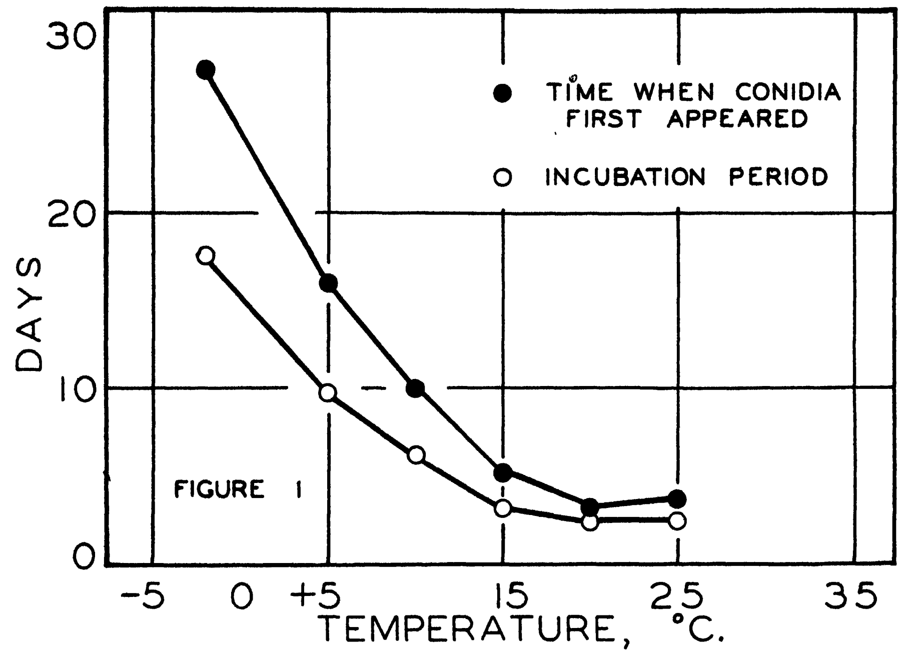


FIG. 1. Time required for development of mildew infection on wheat plants at different temperatures.

(table 2). In another experiment, plants were grown at 20° C until the first leaf was expanded. Then the plants were inoculated. Half the pots were kept at that temperature, while the remainder were removed to a thirty-degree chamber. Each morning and evening (8:30 a.m. and 6:30 p.m.) thereafter, two pots from each set were exchanged—i.e., two from the lower temperature were removed to the thirty-degree chamber and vice versa. The results are presented in table 2.

Two-and-one-half days after inoculation the plants continuously at the lower temperature from the start had minute patches of mycelium on them and one-and-one-half days later numerous conidiophores. Plants left at 20° C less than forty-eight hours before transference to 30° C showed no macroscopic signs of infection after four to five-and-one-half days at the higher

TABLE 2. *Effect of transferring plants grown at moderate and high temperatures to high and moderate temperatures, respectively, at regular intervals after inoculation*

Days at 20° C after inoculation	Development of mildew on plants grown at 20° C and transferred to 30° C at regular intervals after inoculation
0.0	No macroscopic signs of mildew on any of these plants after 5.5 days
0.5	" " " " " " " " " " " 5.0 "
1.0	" " " " " " " " " " " 4.5 "
1.5	" " " " " " " " " " " 4.0 "
2.0	Small white tufts of mycelia present after 3.5 "
2.5	" " " " " " " 3.0 "
3.0	" " " " " and a few conidia after 2.5 "

Days at 30° C after inoculation	Development of mildew on plants grown at 30° C and transferred to 20° C at regular intervals after inoculation
0.0	Few small mycelial patches present after 2.5 days, conidia after 3.5 days
0.5	" " " " " " 2.5 " , " " " "
1.0	" " " " " " 3.0 " , few conidia after 5.0 days
1.5	No mildew development macroscopically apparent after 5.0 days
2.0	" " " " " " 5.0 "
2.5	" " " " " " 5.0 "
3.0	" " " " " " 5.0 "

temperature. Those transferred after forty-eight or sixty hours had only minute white flecks after an additional eighty-four or seventy-two hours, respectively, at the higher temperature. These plants were then returned to the lower temperature, but no further development of the mildew occurred. Microscopic examination showed the hyphae to be shrunken and shriveled. Plants removed from 30° to 20° C twelve hours after inoculation developed mycelial patches on their leaves two and a half days later or three days after inoculation. These plants never became so heavily infected as those at a favorable temperature from the start. Evidently a few spores and germ tubes were capable of withstanding the high temperature for several hours and when they were placed in favorable conditions they established infection. Similarly, plants at 30° C for twenty-four hours after inoculation showed sparse mycelia three days later, or four days after inoculation. A few conidia appeared six days after inoculation. From these results it seems safe to conclude that the harmful effect of high temperatures is primarily a direct one on the fungus and that the host plant is not directly involved.

Figure 2 indicates the effect of temperature upon the germination of conidia in tap water. A net micrometer was used for counting, and only spores within a given area in the center of each drop were counted. This precaution reduced the error which might have arisen, from differential exposure of spores in different regions of the drop, if all spores in a given drop had been counted. The controls indicated that about 1.5 per cent of the spores in a drop might already have germinated at the time of mounting the prepa-

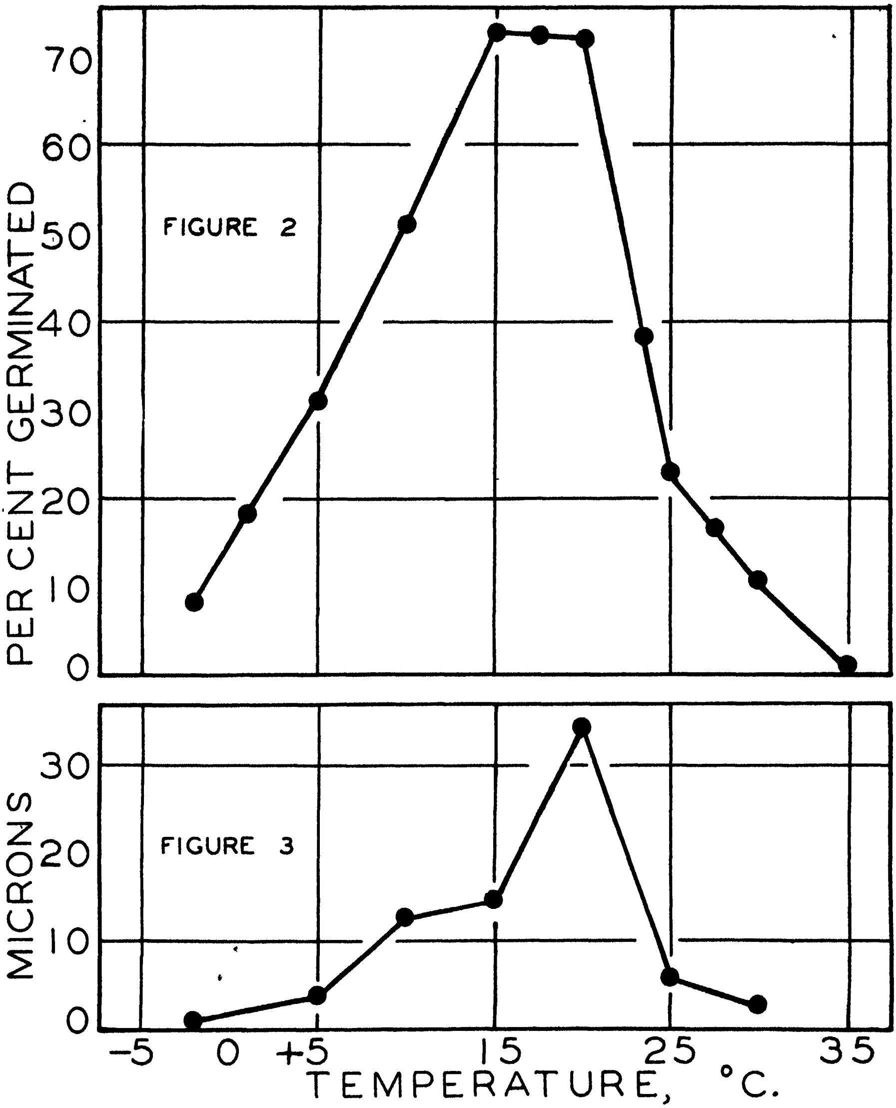


FIG. 2. Influence of temperature upon germination of powdery mildew spores after 24 hours in tap water. FIG. 3. Influence of temperature upon growth of the germ tube of powdery mildew conidia in tap water 48 hours.

ration. Therefore germination percentages below this figure,—i.e., 35° C—represent no germination at all. A comparison of figures 1 and 2 shows that infection does not occur over as wide a range as germination. This is due to failure of the parasite to penetrate into the host tissue at temperatures over 25° C.

The hanging drop method of investigating spore germination has been subjected to adverse criticism by Duggar (1901), Doran (1922), and McCallan and Wilcoxon (1932). However, since large numbers of spores distributed in many drops were used and since the figures obtained were easily reproduced in later experiments under similar conditions, it seems reasonable to consider the data that are plotted in figure 2 reliable.

Perhaps, as Brown (1922) has suggested, a more accurate measure of the early growth and development of a fungus is obtained from the average length of the germ tubes than from the percentage of germination. Figure 3, in which the average germ-tube length in microns after 48 hours is plotted against the temperature is intended to show the relation of temperature to the early growth of *Erysiphe* as indicated by this criterion. Spores were mounted in hanging drops of tap water and measurements were made forty-eight hours after mounting. After longer periods of time it was impossible to measure accurately the specimens at 15°, 20°, and 25° C. Mycelia of *Erysiphe graminis* regularly penetrate a susceptible wheat leaf in twenty-four to seventy-two hours depending on the temperature. These data show that by this criterion also the optimum temperature is 20° C and that as the temperature differed from that value the mildew growth decreased. The decrease in growth was, however, far more abrupt above 20° C than below that point. The data plotted in figures 2 and 3 are essentially alike in that development drops off more abruptly above the optimum than below it. The germination curve, however, indicates a wider optimum range than the one for early growth of the fungus.

SUMMARY

A study was made of the effect of temperature upon the infection of wheat (*Triticum vulgare*) by the powdery mildew, *Erysiphe graminis tritici*. Under the conditions of the experiments (12 hours of illumination daily from a 1000 watt Mazda lamp and high relative humidity) infection occurred from −2° to 25° C. The optimum temperature for infection was 20° C. No macroscopically visible signs of infection were observed above 25° C.

Spores of the fungus suspended in tap water germinated readily from −2° to 30° C. The optimum temperature for the germination of spores and for growth of the young germ tubes was 20° C.

Failure of wheat plants to become infected at 30° C was due to inability of the young fungus mycelium to tolerate the high temperature.

UNIVERSITY OF CALIFORNIA COLLEGE OF PHARMACY
SAN FRANCISCO, CALIFORNIA

Literature Cited

Brown, W. 1922. On the germination and growth of fungi at various temperatures and in various concentrations of oxygen and of carbon dioxide. Ann. Bot. 36: 257–283.

Doran, W. L. 1922. Effect of external and internal factors on the germination of fungous spores. Bull. Torrey Club **49:** 313–340.

Duggar, B. M. 1901. Physiological studies with reference to the germination of certain fungous spores. Bot. Gaz. **31:** 38–66.

Maneval, W. E. 1922. Germination of teliospores of rusts at Columbia, Missouri. Phytopathology **12:** 471–488.

Marchal, E. 1902. De la specialisation du parasitisme chez *l'Erysiphe graminis.* Compt. Rend. **135:** 210–212.

McCallan, S. E. A. & Wilcoxon, F. 1932. Precision of spore germination tests. Contr. Boyce Thompson Inst. **4:** 233–243.

Neger, F. W. 1902. Beiträge zur Biologie der Erysipheen. Flora **90:** 221–272.

Trelease, S. F. 1925. Chamber with thermostatic control and rotating table for plant cultures. Bull. Torrey Club **52:** 389–395.

Trelease, S. F. & Trelease, H. M. 1928. Susceptibility of wheat to mildew as influenced by salt nutrition. Bull. Torrey Club **55:** 41–68.

Yarwood, C. E. 1934. The comparative behavior of four clover-leaf parasites on excised leaves. Phytopathology **24:** 797–806.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 386–397 JULY, 1943

NOTES ON PLANTS OF THE PACIFIC ISLANDS—III[1]

F. R. FOSBERG

In this paper are presented taxonomic, nomenclatural, and distributional notes on plants from the Hawaiian Islands, the New Hebrides, and Christmas Island. New species, varieties, combinations, or names are proposed in *Anectochilus, Gouldia, Timonius, Coprosma,* and *Dubautia,* with general notes on *Nephrolepis, Adiantum, Lygodium, Azolla, Cyperus, Portulaca, Spergularia, Leucaena, Phaseolus, Abutilon, Hibiscus, Malachra, Maurandya, Ruellia, Gouldia, Coprosma, Borreria, Richardia, Elephantopus, Pseudelephantopus, Ageratum,* and *Solidago.* Herbarium abbreviations are BISH for Bishop Museum, F for Field Museum, A for Arnold Arboretum, D for Otto Degener private herbarium, HARV for Harvard Botanical Museum, US for U. S. National Herbarium, and USNA for U. S. National Arboretum.

POLYPODIACEAE

NEPHROLEPIS BISERRATA (Sw.) Schott. This is the fourth species of this genus to be found in the HAWAIIAN ISLANDS. It was found growing on OAHU, probably indigenous, in a small pit in coral limestone on the Ewa Coral Plain, Jan. 12, 1936, *Fosberg 12806* (BISH) (det. R. C. Benedict).

NEPHROLEPIS BISERRATA var. FURCANS Hort. This remarkably stable horticultural variety has become established and forms a considerable colony around the abandoned settlement at the mouth of Wailau Valley, MOLOKAI, Dec. 28, 1936, *Fosberg 13453* (BISH) (det. R. C. Benedict).

NEPHROLEPIS CORDIFOLIA (L.) Presl. Although this species has been commonly regarded by previous writers as introduced in the HAWAIIAN ISLANDS, its frequent occurrence as a part of the undisturbed cloud forests of the mountain ranges, and its absence from the lowlands indicate that it is in all probability native. This fern was reported from the Hawaiian Islands by Edward Bailey in *Hawaiian Ferns,* 48 (1882). The following collections (except *Topping 3808*) were kindly determined by R. C. Benedict. LANAI: Lanaihale ridge, *Fosberg 12437* (BISH). MOLOKAI: top of cliff at head of Wailau Valley, *Fosberg 13368* (BISH). OAHU: Koolau Mts.: top of cliffs at head of Haiku Valley, Heeia, *Fosberg 13870* (BISH); peak at head of Waiawa trail, *Fosberg & Hosaka 13912* (BISH); main divide between Waikane Valley and Waikakalaua Gulch, *Fosberg & Hosaka 13928* (BISH); main divide near top of Castle Trail, Kaipapau, *Fosberg & Hosaka 13954* (BISH); crest of mountains above Kaipapau Gulch, *Fosberg & Egler 14227* (BISH); Laie Trail, Kakawainui-Ihiihi ridge, Laie, *Fosberg 14235* (BISH, USNA); Mauka Laie, Gold Brick Hill, *Topping 3808* (USNA).

[1] See Bull. Torrey Club 65: 607–614. 1938; 67: 417–425. 1940.

KEY TO HAWAIIAN SPECIES OF NEPHROLEPIS

A. Pinnules linear-lanceolate, attenuate toward apex, frond flat.
  B. Rhachis densely tawny or rusty woolly . *N. hirsutula* (Forst.) Presl (on the basis of Degener, Flora Hawaiiensis 17: NH, 9/9/'38 and of *Topping 2705* (USNA))
  BB. Rhachis not densely woolly, somewhat scaly or scurfy. *N. biserrata* (Sw.) Schott (form with apices of pinnules forked is var. *furcans* Hort.)
AA. Pinnules oblong or oblong-lanceolate, acute to rounded at apex.
  C. Frond flat, narrow, 5 cm. or less wide, glossy above, pinnules oblong, rhachis densely covered with red-brown scales, stolons often tuberiferous . *N. cordifolia* (L.) Presl
  CC. Frond trough-shaped, usually broader, rhachis thinly tawny scaly, stolons not tuberiferous . . . *N. exaltata* (L.) Schott

ADIANTUM CUNEATUM Langsd. & Fisch. Some of the Hawaiian material commonly referred to *Adiantum capillus-veneris* L., regarded as native in the islands, is to be referred to the introduced *A. cuneatum*, probably escaped from cultivation. Dr. W. R. Maxon informs me that a reliable key character for distinguishing the two is that in *A. cuneatum* the veins of the sterile pinnules end in the sinuses between the teeth while in *A. capillus-veneris* they end at the apices of the teeth. Completely fertile specimens are often difficult to determine.

HAWAIIAN ISLANDS: HAWAII: Hills above Akaka Falls, Honomu, Dec. 8, 1933, *Fosberg 10470* (BISH, USNA). OAHU: Carter Ranch, upper Manoa Valley, Honolulu, Sept. 26, 1932, *Fosberg 8861* (BISH, USNA); Niu Valley, June 4, 1932, *Topping 3532* (USNA); Honolulu, cultivated, April 1, 1933, *Fosberg 9376* (BISH, USNA).

SCHIZAEACEAE

LYGODIUM JAPONICUM Sw. This climbing fern may be reported as semi-established around an old garden at Puueo, Hilo, HAWAII, Aug. 6, 1936, *V. O. Fosberg 34* (BISH).

SALVINIACEAE

AZOLLA FILICULOIDES Lam. This floating water fern appeared in the taro patches and irrigation ditches of OAHU about 1934, and soon became extremely abundant. H. L. Lyon has told me that in 1926 he introduced *Azolla caroliniana* into the islands at the request of the mosquito abatement committee. The latter plant evidently did not become established, though the one now common in the taro patches has been misidentified as that species. Examination of fruiting specimens (*Fosberg 13833*) of the plant now in the islands shows that it is *A. filiculoides*, which has, among other characters, non-septate glochidia or barbed hairs on the microspore masses, rather than septate ones as in *A. caroliniana*.

HAWAIIAN ISLANDS: OAHU: Honolulu, Waikiki, *Fosberg 13815* (BISH); Honolulu, Manoa Valley, May 22, 1937, *Fosberg 13833* (BISH, USNA).

ORCHIDACEAE

Anectochilus apiculatus L. O. Williams and F. R. Fosberg, sp. nov. Herba pallide viridis; flos pallide flavo-viridis, calcari extus non valde

geminato, mesochilo subtus laterale bidentato, anthero apiculato, mesochilo epichiloque quam in *A. sandvicenso* valde brevior.

Pale green herb with succulent ascending or subdecumbent stems up to 25 cm. long, 3–5 mm. thick, glabrous except the inflorescence, prostrate and rooting at nodes in lower portion; leaves ovate to elliptic-ovate, 5–8 cm. long, 2.5–4 cm. wide, apex obtuse to acutish, base rounded to subcordate, narrowed to a distinct membranous petiole 3–10 mm. long, expanded and inflated below into an amplexicaul sheath about 1 cm. long on the petiolar side, 4 mm. long on the reverse, lamina membranous; spike 5–10 cm. long on a peduncle 3–5 cm. long, uppermost 1 or 2 leaves reduced to bracts; flowers somewhat loosely arranged, subtended by ovate scarious membranous bracts about 10 mm. long, about as long as the ovary and enclosing it at base; flowers pale yellowish green, about 12–15 mm. long, ovary lance-ovoid, about 10 mm. long, 1.5–2 mm. thick near base, apex subacuminate, tending to be incurved, dorsal sepal ovate, 4.5 mm. long, blunt and slightly cucullate at apex, lateral sepals 6 mm. long (over all), obliquely oblong-orbicular, obtuse, with base obliquely cordate, greatly enlarged on lower side, this basal lobe subsaccate, margins entire, texture membranous; petals 4.5 mm. long, sublunate-ovate, bluntly subacuminate, membranous, margins erose; lip 7.5 mm. long, with a short pouch-like spur 2 mm. long, enclosed by the bases of the sepals, spur scarcely geminate externally, divided within into two cavities by a longitudinal septum, each cavity containing a suberect finger-shaped callosity, mesochile 5 mm. long, about 1.5 mm. wide but inrolled into a tube, with 2 forward-pointing pairs of sub-fleshy teeth about two thirds the distance from base on lower side of the mesochile, distal pair 0.75 mm. long, lower pair 0.5 mm. long, epichile obcordate, 4 mm. wide, 2.5 mm. long, sinus 1.5 mm. deep, lobes rounded; column 2.5 mm. long; anther ovate, 3 mm. long, somewhat apiculate, twisted slightly to one side, brown with whitish margins, cymbiform; fruit fusiform, 1 cm. long, 3 mm. thick, green.

HAWAIIAN ISLANDS: MOLOKAI: head of Wailau Valley, trail up Waiakeakua-Waiokeela ridge, on steep ridge shaded in wet forest, alt. 750 m., Dec. 27, 1936, *Fosberg 13448* (HARV—TYPE, USNA, BISH).

This species may be distinguished from the commoner *A. sandvicensis* by its smaller, greenish rather than bright yellow flowers, lip with spur not conspicuously geminate externally, with mesochile conspicuously shorter and with two pairs of subfleshy teeth on the lower side rather than many or no membranous ones, with epichile much shorter, and the anther apiculate rather than acute.

A somewhat similar plant was found in wet woods in the mountains behind Hauula, Oahu, some years ago by Mr. H. Morley, but the specimen was unfortunately lost.

CARYOPHYLLACEAE

SPERGULARIA MARINA (L.) Griseb. Spic. Fl. Rummel, et Bith. **1**: 213. 1843. *Arenaria rubra* β marina L. Sp. Pl. 423. 1753. *Arenaria marina* Allioni, F. Pedem. **2**: 114. 1785. *Spergularia salina* J. & C. Presl, Fl. Cech. 95. 1819.

The correct name for the plant referred by me to *Spergularia salina* in a previous paper (Occ. Pap. Univ. Haw. **32**: 5. 1937) is *S. marina*. For further synonymy and discussion see Rossbach, Rhodora **42**: 123–137 (1940).

MALVACEAE

MALACHRA ALCEIFOLIA Jacq. Collect. **2**: 350. 1788; Ic. Rar. **3**: *pl. 549.* 1786–1793. *Malachra rotundifolia* Schrank, Pl. Rar. Hort. Mon. *pl. 56.* 1819.

A coarse, hispid herbaceous perennial 0.5–2 m. tall; stems with close stellate pubescence as well as sparse long stiff hairs; leaves 7–10 cm. across, roundish in general outline, shallowly 5-lobed, palmately veined, subcordate, obtuse or acutish, irregularly serrate, somewhat pubescent on veins, petioles 5–9 cm. long, closely stellate-pubescent; stipules filiform, about 15 mm. long, sparsely hirsute; flowers yellow, in compact axillary clusters on peduncles up to 15 mm. long, these densely stellate-pubescent, clusters surrounded by 3–4 broadly cordate bracts, these somewhat lobed, acute, sparsely hirsute, variegated; flowers few in a cluster, calyx about 6 mm. long, tube white, striped with brown, lobes lanceolate, long-hirsute; corolla hairy 12–15 mm. long; stigmas irregular in shape, ovary 5-celled, ovules 1 in a cell; fruit subglobose, splitting into 5 parts, these 3 mm. long, larger distally, puberulent, light brown with darker reddish-brown veins, splitting open along the lower two thirds of the inner angle; seeds dull sooty brown, same shape as carpel, free from carpel wall.

HAWAIIAN ISLANDS: OAHU: Kawailoa School, Waialua, Oct. 1936, *A. Miyake* (BISH, USNA).

Found growing in a vacant lot; a native of tropical America evidently recently introduced into Hawaii.

SCROPHULARIACEAE

MAURANDYA ERUBESCENS (Don) Gray. The plant usually called *Maurandya scandens* in the Hawaiian Islands, an introduced vine with densely pubescent leaves, has been identified by Dr. F. W. Pennell as *M. erubescens*, a native of Mexico. The true *M. scandens* is a glabrous plant.

HAWAIIAN ISLANDS: HAWAII: Volcano Road near Naalehu, alt. 200 m., *Fosberg 10140* (BISH, USNA). OAHU: near H. S. P. A. Arboretum, Carter Ranch, Manoa Valley, *Fosberg 8859* (BISH, USNA), *Fosberg & Duker 8940* (BISH).

ACANTHACEAE

RUELLIA GRAECIZANS Backer, Brittonia **3**: 85. 1938. This plant has been called *R. amoena* Nees and *R. ventricosa* Kunth, but neither of these names is valid. It is a small herbaceous species with dark green ovate to lanceolate leaves and horizontal tubular red flowers. It has become rather common as a garden weed in various parts of Honolulu and has been said to occur on Maui, but the Maui report is not substantiated by a specimen. I am indebted to Mr. E. C. Leonard for calling my attention to Backer's publication.

HAWAIIAN ISLANDS: OAHU: Honolulu, *Fosberg 14222a* (BISH).

RUBIACEAE

GOULDIA Gray. Since the publication of my revision of this Hawaiian genus (Bish. Mus. Bull. **147**: 1–82. 1937) the following observations have accumulated, and a number of typographical errors have been detected, which are here listed with corrections.

p. 4—footnote—for 181 read 81
p. 19—line 23—for 77 read 80
p. 20—line 9—for 58 read 62
line 11—for 62 read 58
line 46—for 58 read 61
p. 21—line 2—for 82 read 97
line 7—for 40 read 43
p. 22—line 45—for 82 read 83
line 49—for 81 read 82
p. 43—line 17—for 12782 read 12781
p. 25—in the synonymy of *Gouldia terminalis* insert *Hedyotis chamissoniana* Steud. Nom. ed. 2, 1: 727, 1840.

GOULDIA on the island of LANAI: The recovery of the forests on the island of Lanai after almost complete destruction by introduced grazing animals (see Fosberg, Mid-Pacific Mag. April–June **1936**: 119–123. 1936) has, in all probability, resulted in a forest of considerably different floristic composition from that originally existing there. However, there is no way of demonstrating this conclusively, as we know little about the original forest.

During a visit to Lanai in 1935 I made rather extensive collections of *Gouldia*, making a particular search for the several varieties known from earlier collections. It was thought that a search especially for *Gouldia* should easily reveal all varieties which had turned up previously in more general collecting.

Complete identification of the specimens collected on this trip has shown that some varieties are very rare, while one was not found at all. *G. terminalis* var. *pseudodichotoma* was represented only by *Fosberg 12411; G. terminalis* var. *lanai* only by *Fosberg 12579; G. terminalis* var. *subcordata* by three collections, *Fosberg 12599, 12412,* and *12606. Fosberg 12502* seems to be a hybrid, *G. terminalis* var. *subcordata* × var. *pseudodichotoma,* and *Fosberg 12572* another, *G. terminalis* var. *subcordata* × var. *bobeoides. G. terminalis* var. *bobeoides* was not represented at all in the collection excepting possibly as one parent of this latter hybrid and one mentioned below. The above collections all came from the gulches, in sheltered localities.

The plants from the ridges and summits, where *Gouldia* was quite abundant, were, with the exception of one collection, all *Gouldia st.-johnii* var. *munroi* or hybrids between this and varieties of *G. terminalis.* All collections of *G. st.-johnii* var. *munroi* numbering fourteen, came from ridges and summits, where some grew in much-exposed places. It is one of the really abundant plants in the scrub forest that is revegetating these ridges. Whether in the original forest this distribution was characteristic, or whether *G. st.-johnii* is a very aggressive plant and especially able to colonize denuded areas is difficult to know. Unfortunately we have a very incomplete picture of the original forest covering of Lanai. It should be remembered that *G. st.-johnii* var. *typica,* of Oahu, is a plant of exposed ridges and summits.

Of hybrids involving *G. st.-johnii* var. *munroi* two were represented by one collection each and were found in gulches only. These were *G. st.-johnii* var. *munroi* × *terminalis* var. *bobeoides* (?), *Fosberg 12495,* and *G. st.-johnii* var. *munroi* × *terminalis* var. *lanai, Fosberg 12584. G. st.-johnii* var. *munroi* × *terminalis* var. *pseudodichotoma* is represented by four collections, nos. *12398, 12373, 12484,* and *12594.* The first three were on ridges, the last in a

gulch bottom. *G. st.-johnii* var. *munroi* × *terminalis* var. *subcordata* is represented by *Fosberg 12477* and *12482*, both from ridges.

A set of all the above collections is deposited in the Bishop Museum.

One collection, from a rather dry ridge, proves to be the following previously described form of *G. terminalis* var. *ovata:*

GOULDIA TERMINALIS var. OVATA f. **obovata** Fosberg, f. nov. Arbor glabra, ramulis angulatis; folia obovata coriacea; thyrsus hemisphaericus, pedunculis suberosis.

Tree up to 3 m. tall, branchlets strongly angled, internodes 0.5–2 cm. long, mostly about 1 cm., branches appearing dichotomous through the death of terminal inflorescences and development of a pair of branches from the basal node; leaves obovate, up to 6 cm. long and 3 cm. wide, coriaceous, apex obtuse to rounded, base strongly and abruptly contracted, obtuse to rounded, margin revolute, petiole up to 1 cm. long, about 1 mm. thick; stipules strongly carinate; thyrse hemisperical, up to 4 cm. long and 3 cm. wide, peduncle corky in fruit; flowers not known; fruit less fleshy than usual in this genus.

HAWAIIAN ISLANDS: LANAI: ridge below Puu Aalii, between Maunalei and Hauula drainages, rather dry forest, alt. 800 m., Nov. 30, 1935, *Fosberg 12472* (USNA—TYPE, BISH).

Differs from f. *euovata* in the smaller, plane, broadly obovate leaves, rounded or obtuse at both ends. This form extends the distribution of var. *ovata* to Lanai, where it seems logical that it should be found.

GOULDIA TERMINALIS var. OVATA f. SANTALIFOLIA Fosberg. Material collected by *Degener*, no. *12522b* (D, USNA), from southeast ridge of Iao Valley, west MAUI, HAWAIIAN ISLANDS, gives this form a somewhat broader distribution than known formerly. Heretofore, on Maui it has only been found in Olowalu Valley. The leaves of this collection are somewhat broader than is usual in this form, and not folded.

Degener's no. *12522* contained two sheets of f. *santalifolia*, several sheets of *G. terminalis* var. *cordata* f. *eucordata*, and a considerable number of sheets of a form that seems to be a hybrid between them. The latter is so distinctive in appearance that, had not the two presumed parents been present, I should probably have described it as a new form of var. *ovata*. It is glabrous, with angled long branchlets as in var. *cordata*, oblong to elliptic leaves and small spherical thyrses as in f. *santalifolia*, these appearing very compact. The node at the base of the thyrse, in many specimens, gives rise to two leafy branches, a character not common in the parents but suggesting var. *pseudodichotoma* of Lanai.

GOULDIA TERMINALIS var. PARVULA f. **impressa** Fosberg, f. nov. Arbor, ramulis non valde condensatis; folia oblonga vel obovata, obtusa, subtus pilosa.

Tree 15 feet tall, trunk 8 inches thick, branchlets strongly hirtellous, not strongly reduced, internodes 5–10 mm. long even in terminal portions; leaves oblong to obovate, up to 3.5 (rarely 5) cm. long, 2 (rarely 2.5) cm. wide, usually about half that size, obtuse or rounded at both ends, blade conspicuously pilose beneath, veins strongly impressed above, petiole 2–5 mm. long, glabrous.

HAWAIIAN ISLANDS: MAUI (east): Paliku, Haleakala, Aug. 5, 1939, *Degener 12521* (D—TYPE).

This form seems intermediate between f. *euparvifolia* and f. *subpilosa*, having the abundant pubescence and smaller leaves of the former, and the open habit of the latter, and differs from both in having both the apex and base of the leaves obtuse or rounded.

GOULDIA TERMINALIS var. PUBESCENS × var. PARVIFOLIA f. IMPRESSA. Like f. *impressa* but branchlets pubescent, internodes more elongate, leaves larger, more pubescent beneath.

HAWAIIAN ISLANDS: MAUI (east): Paliku, Haleakala, *Degener 12526* (D, USNA).

This is probably the correct disposition of this collection. The petioles are a trifle long for either parent. Perhaps a form of var. *ovata* may be involved, but none is known from this vicinity. Satisfactory disposal of the Gouldias from Maui awaits an opportunity for a careful field survey and extensive collecting.

GOULDIA TERMINALIS var. KAPUAENSIS f. **violetae** Fosberg, f. nov. Ramuli rigidi teretes, minute hirtelli; folia oblanceolata vel anguste elliptica, obtusa vel acuta, coriacea, subtus hirtella; thyrsus hirtellus; hypanthium hirtellum.

Shrub 1.5 m. tall, branchlets stiff almost to the tips, terete, minutely hirtellous; leaves oblanceolate to narrowly elliptical, up to 10 cm. long, 3 cm. wide, apex obtuse to subacute, coriaceous, hirtellous beneath, especially on the midrib, margin closely revolute, petiole up to 14 mm. long, about 1 mm. thick; thyrse about 2 cm. long, hirtellous; hypanthium somewhat hirtellous.

HAWAIIAN ISLANDS: HAWAII: Kau, between west and east arms of the 1907 flow, on dry lava, Aug. 10, 1936, *V. O. Fosberg 49* (BISH—TYPE).

Much like f. *pittosporoides* but very hairy and differing somewhat in leaf shape and slightly longer petiole. Named for the collector, Violet O. Fosberg.

GOULDIA TERMINALIS var. MACROCARPA f. CUNEATA Fosberg. Degener's collection cited below contains material with relatively large, somewhat obovate leaves 5–7 cm. long and 2.5–3.5 cm. wide, with the midribs hirtellous beneath, and also specimens with small oblong, somewhat revolute leaves, not so hirtellous, 3–4 cm. long, 1.5–2 cm. wide. These could scarcely have come from the same tree. The larger-leafed specimen corresponds well with f. *cuneata*, though the leaf bases are scarcely cuneate. This is a marked extension of the range of this form, known previously only from the plateau and western slope of the mountain of Kauai.

The small-leafed portion of this collection might be placed in f. *sclerophylla*, though the leaves are too thin and mostly too pubescent. It seems more likely, because of the restricted known distribution of f. *sclerophylla* and the discrepancies in leaf thickness and pubescence, that it is a hybrid between var. *macrocarpa* f. *cuneata* and var. *osteocarpa*, which latter is known to be widespread at low elevations on Kauai. The small-leafed plant is in flower while the large-leafed one has fruits which are enlarged because of insect attack.

HAWAIIAN ISLANDS: KAUAI: Kalualea, Koloa, alt. 1500 ft., *Degener & Ordonez 12645a* (large-leafed) and *12645b* (small-leafed) (D, USNA).

GOULDIA HILLEBRANDII var. NODOSA Fosberg. Two Degener specimens, collected near Mt. Eke, MAUI, HAWAIIAN ISLANDS, July 2, 1927, have the thyrses glabrous or almost so and seem in almost every other respect to fit var. *nodosa* rather than var. *typica*. One of them has the budding thyrses below the leaves, the other is in fruit. With the exception of the position of the inflorescences, a rather weak character, they match var. *nodosa* and may be regarded as extending the range of this variety to Maui.

Timonius kajewskii (Guill.) Fosberg, comb. nov. *Guettarda kajewskii* Guillaumin, Jour. Arnold Arb. **13**: 6. 1932.

This species, described from flowering material from the NEW HEBRIDES, Aneityum, *Kajewski 724* (A—TYPE, US), was known to its author in flower only. Another specimen, *Kajewski 826* (A, US), collected at the same locality, referred to *Guettarda* sp. by Guillaumin, is vegetatively identical, but bears peduncles with single fruits subtended by 2 vestigial bracts. The purple fruits are cylindrical, somewhat compressed, and with the apex prolonged to a point. They have the 12 cells sclerified, arranged in two parallel rows and fused into a ribbed stone. There seems little doubt that this plant is a fruiting specimen of Guillaumin's species, and that it should be referred to the genus *Timonius*, where its nearest relative is *T. smithii* Fosberg of Fiji (see Fosberg, Sargentia **1**: 121. 1942).

COPROSMA Forst.

Oliver's key (Bish. Mus. Bul. **132**: 28. 1935) separates *C. elliptica* from the *C. montana* group by the following contrast of characters:

Leaves with few secondary nerves, under 20 mm. long	*C. elliptica.*
Leaves penninerved; over 20 mm. long	Group of *C. montana.*

Although this will correctly separate the majority of specimens, my collections of *C. montana* var. *crassa*, nos. *9940* and *9977* (BISH), both from the upper part of Haleakala, MAUI, HAWAIIAN ISLANDS, and even a collection of *C. ochracea* var. *typica*, no. *10036* (BISH, USNA) from Puu Kukui, MAUI, have such small leaves and few nerves that they would go into *C. elliptica*, which they do not resemble. The following supplementary key will separate these small-leafed forms:

Ultimate branchlets 1–1.5 mm. thick	*C. elliptica.*
Ultimate branchlets 2 mm. or more thick, stiff.	
Pubescence short, inconspicuous	*C. montana* var. *crassa.*
Pubescence hirsute, dense	*C. ochracea* var. *typica.*

COPROSMA ELLIPTICA Oliver. A collection made in Alakai Swamp, KAUAI, HAWAIIAN ISLANDS, *Fosberg 12764* (BISH, USNA) has the pubescence much more sparse than, according to Oliver's description, the species ordinarily shows.

COPROSMA PUBENS var. TYPICA Oliver. This variety seems to be much more variable than Oliver's discussion (Bish. Mus. Bul. **128**: 171. 1935) would indicate. Of a series of collections from the Haiku Uka Trail, Makawao Dist., MAUI, *Fosberg 9847* (BISH, USNA) has leaves with blades 35–60 mm. long, fruiting peduncles up to 20 mm. long, bearing either 1 or 3 clusters of orange colored fruits; *Fosberg 9881* (BISH, USNA) has even smaller leaves, and peduncles tending to be slightly compound, fruits globose, 5–6

mm. across, orange; *Fosberg 9851* (BISH, USNA) has peduncles up to 30 mm. long, rarely compound, when simple having an articulation part way up bearing a small stipular sheath.

COPROSMA LONGIFOLIA Gray var. **longifolia** (Gray) Fosberg, nom. nov. *Coprosma longifolia* Gray, Proc. Am. Acad. **4**: 48. 1860.

This is the typical element of the species as described by Gray and restricted by Oliver (Bish. Mus. Bull. **132**: 177–179. 1935). It is common in the wetter regions of both mountain ranges on OAHU.

COPROSMA LONGIFOLIA Gray var. **oppositifolia** Fosberg, var. nov. Folia opposita, flos staminatus tubo corollae exserto lobis subaequalis 2–3 mm. longis, antheribus 4 mm. longis.

Leaves opposite, elliptic-lanceolate; stipular sheath 3–5 mm. long, appressed-hirtellous near base, with lobes 2–4 mm. long, somewhat acuminate, ciliate, glandular-denticulate; peduncle of staminate inflorescence 3–5 mm. long, bracts elliptic or ovate, corolla of staminate flowers funnelform, tube definitely exserted, strongly contracted below the expanded throat, tube plus throat 5–6 mm. long, lobes 6, subequal, 2–3 mm. long, bluntly lanceolate; anthers 6–8, linear-oblong, apiculate, lobed at base, 4 mm. long; pistillate flowers and fruit unavailable.

HAWAIIAN ISLANDS: OAHU: Waianae Mts., Makaha-Waianae Kai, Puu Kawiwi-Puu Kaala ridge, in wet forest, alt. 1150 m., March 31, 1935, *Fosberg 10855* (USNA—TYPE, Bish, A, F).

This variety differs most conspicuously from var. *longifolia* in its opposite leaves, definitely exserted corolla tube, much longer corolla throat and shorter peduncle and stipular sheath. From the other opposite leafed member of this group, *C. molokaiensis* St. John, this variety differs in its longer peduncles, the equally 6-lobed, rather than bilabiate, corollas, and shorter anthers. The slightly hirtellous stipules suggest a possibility of hybridization between *C. longifolia* and *C. ochracea* var. *kaalae*, recalling Oliver's suggestion (Bish. Mus. Bull. **132**: 175. 1935) for *C. molokaiensis*. The evidence at hand does not justify a suggestion of such an origin for this variety, but the presence of the two possible parents in the vicinity of the type locality gives reason to look into the matter at some future time.

BORRERIA LEAVIS (Lam.) Griseb. This weed, which is now widespread in the tropical Pacific, is becoming common in the Hawaiian Islands. It is a low plant with pectinate stipules and terminal and axillary densely capitate verticels of small white or pinkish flowers. The fruits are 2-celled capsules, both cells of which are ventrally and apically dehiscent, leaving a sub-persistent septum. In each cell is a single oblong, brown, transversely rugulose seed.

HAWAIIAN ISLANDS: OAHU: Maunawili, Kailua, *Fosberg, Storey, & Oliveira 10772* (BISH, USNA); Woodlawn, Manoa, Honolulu, *Fosberg 14111* (BISH, USNA); Manoa Valley, Honolulu, *Fosberg 10587* (BISH); University Campus, Manoa, Honolulu, *Fosberg 10528* (BISH, USNA).

RICHARDIA BRASILIENSIS (Moq.) Gomez. The plant common in the Hawaiian Islands which is usually referred to *Richardia scabra* L. or *Richardsonia scabra* (L.) St. Hil. really belongs to *R. brasiliensis*. This species was mentioned as occurring in the Hawaiian Islands by Schumann (in Engler & Prantl, Die Nat. Pflanzenf. IV, **4**: 139. 1891). Examination of

fruits of the common Hawaiian weed shows that the nutlets have the ventral face excavated and the general outline heart-shaped. *R. scabra* has cylindrical fruits with an almost closed ventral groove.

HAWAIIAN ISLANDS: KAUAI: Milolii Ridge, Waimea, alt. 2000 ft., *St. John, Fosberg & Oliveira 13739* (BISH, USNA).

COMPOSITAE

ELEPHANTOPUS MOLLIS HBK. According to Dr. S. F. Blake, the plant from Kauai referred to *E. tomentosus* in my paper of 1937 (Occ. Pap. Univ. Haw. 32: 9, 1937) really belongs to *E. mollis*, a native of tropical America that is widespread in tropical regions as a weed.

PSEUDELEPHANTOPUS SPICATUS (Juss.) Rohr. The plant called in the same paper *Elephantopus spicatus* Juss. is, according to Dr. Blake, better regarded as belonging to the genus *Pseudelephantopus*, distinguished by the spicate arrangement of the heads and the peculiarly curved, rather than straight, lateral pappus awns.

AGERATUM HOUSTONIANUM Mill. This garden plant was twice collected growing spontaneously near Honolulu. It may be distinguished from the common *A. conyzoides* L. by its larger heads and lance-linear, densely hairy, rather than oblong, sparingly hairy or glabrous involucral bracts.

HAWAIIAN ISLANDS: OAHU: Nuuanu Valley, June 6, 1937, *Fosberg 14004* (BISH); Manoa Valley, Woodlawn, May 22, 1937, *Fosberg 13835* (BISH); Honolulu, cultivated, *Fosberg 9368* (BISH).

SOLIDAGO ALTISSIMA L. The golden-rod which has escaped from gardens in Nuuanu and Manoa Valleys, Honolulu, has been identified by Dr. S. F. Blake as this species.

HAWAIIAN ISLANDS: OAHU: Honolulu, Nuuanu Valley, Dowsett Tract, Oct. 10, 1936, *Fosberg 13294* (BISH, USNA).

Dubautia sherffiana Fosberg, sp. nov. Frutex ad 0.5 m. altus; foliis alternis, elliptico-lanceolatis; paniculis corymbosis congestis glandulo-pubescentibus; capitulis 6–7 mm. altis, floribus 3–4 exsertis 5-meris, achenis subglabris prismaticis 2.5–3 mm. longis valde costatis, ad basin angustatis.

Shrub 0.5 m. tall, branchlets cylindric, gray, hispidulous, with alternate leaves 4 mm. or less apart, persistent only in the upper 10 cm. of the branchlet; leaves elliptic-lanceolate, 6–7 cm. long, 1–1.5 cm. wide, acute at apex and base, coriaceous, subsessile, appearing glabrous but minutely scabrous on margins, slightly so on under surface, becoming hispidulous toward base, margins somewhat revolute, remotely serrulate in distal half, at broadest part obscurely 11-nerved, nerves occasionally anastomosing to form an irregular and incomplete longitudinal reticulation, the petioliform base appressed to stem for about 2 mm.; inflorescence a crowded terminal corymbose panicle rounded or flattish on top, densely spreading-pubescent and with sparse short gland-tipped hairs, the rhachis up to 5 cm. long, terminating in perfect specimens in a reduced head, or this lacking, panicle branches up to 6–7 cm. long, scattered on the rhachis, subtended by leafy bracts similar to the leaves but greatly reduced, secondary branches subtended by still smaller bracts, on these branches the sessile heads glomerate at the apices, with a few scattered ones further down or with several very small branches

ending in small glomerules, each head closely subtended by a small densely ciliate somewhat ventricose bract; glomerules mostly with 3–6 heads, these 6–7 mm. high, about 2–3 mm. wide above, with 3–4 strongly exserted florets; involucre of 3–4 coherent or slightly connate bracts, narrowly cylindric-campanulate, 3–4 mm. high, 1–1.5 mm. thick at apex, often splitting with the development of the achenes, externally glandular, the free tips densely ciliate, involucral bracts cuneate, the low triangular free portion usually with 1 or 2 small lateral teeth; corolla apparently yellowish-white, 5-lobed, tube about 1–1.2 mm. long, throat abruptly enlarged and campanulate near middle, about 1.7–2 mm. long, lobes ovate, strongly recurved, at least in age, 1–1.3 mm. long; anther tube straw-colored, about 1.3 mm. long, partly or completely exserted, the terminal appendages ovate; achenes prismatic, 2.5–3 mm. long, 0.5–0.6 mm. thick at apex, tapering to base, about 8-ribbed (some ribs very prominent, others less so, sometimes 1 or 2 obscure), dark gray, very sparsely pilosulose toward apex, surface slightly roughened; pappus of a single series of about 25 plumose aristae 2.5–3 mm. long, united at extreme base, brownish-white.

HAWAIIAN ISLANDS: OAHU: Waianae Mts., brushy ridge east of 2nd gulch east of Kaupakuhale, Mokuleia, Oct. 23, 1932, *St. John & Fosberg 12161* (USNA—TYPE). "Great Crater, Hawaii," *U. S. Exploring Expedition* (US) (part, vide infra).

Named for Dr. E. E. Sherff of Chicago, monographer of *Dubautia* and *Railliardia.*

This species is so abundantly distinct that it is difficult to relate it to any particular known species. It belongs with the group called by Gray, and later by Sherff, section *Nervosae* of the genus *Railliardia*, which genus has been reduced to *Dubautia* by Keck (Occ. Pap. Bish. Mus. **11**: (19): 24–28. 1936). In Sherff's treatment of *Railliardia* (Bish. Mus. Bull. 135: 106–136. 1935) *D. sherffiana* keys nearest *R. lonchophylla* Sherff [*Dubautia lonchophylla* (Sherff) Keck], which it does not resemble, or to *R. reticulata* Sherff [*Dubautia reticulata* (Sherff) Keck], but differs from the latter in having alternate subglabrous leaves, instead of opposite white-hispid ones, sessile, much shorter, fewer-flowered heads, practically glabrous instead of white-hispid achenes, and other less important characters. *D. reticulata* is known only from Maui.

Sherff credits only two species of *Railliardia* to Oahu—*R. scabra* [*Dubautia scabra*] of which I can find no citation of a specimen and *R. linearis* [*D. linearis*] of which one U. S. Exploring Expedition collection from Kaala is cited. Of these, *D. linearis* comes closest to *D. sherffiana* but differs in having its leaves narrower, only 3- to 5-nerved, and ternate instead of alternate; heads usually pedicellate instead of sessile, with 4–8 florets instead of 3–4 and pubescent involucres. Although Sherff says that the florets of *R. linearis* are included, examination of all of the material in the U. S. National Herbarium shows that they become quite well exserted when reasonably mature. In small size the heads of *D. sherffiana* are approached only by those of *D. linearis,* and this may probably be its closest relative, though this is by no means a final decision. I have not seen the Oahu specimens of *D. linearis* cited by Sherff, but assume that they are correctly placed. On one sheet of the U. S. Exploring Expedition material (US) said to be from "Great Crater, Hawaii" are 2 twigs. One is typical *D. linearis,* while the other has alternate,

much larger, 7-nerved lanceolate leaves, and mostly sessile, only slightly puberulent involucres. It undoubtedly belongs in *D. sherffiana,* and may well have come from Oahu, as the localities on the U. S. Exploring Expedition specimens were often woefully confused.

CHRISTMAS ISLAND

A number of species may be added to the known flora of Christmas Island on the basis of my collections made there in August 1936. The following are not in Christophersen's annotated list (Bish. Mus. Bull. 44: 22–27, 1927). All except *Abutilon indicum* and possibly *Portulaca fosbergii* appear to be introduced.

CYPERUS ROTUNDUS L. A small colony in the village, London, *Fosberg 13282* (BISH).

PORTULACA FOSBERGII Von Poelln. Paris, *Fosberg 13269* (BISH, USNA) (det. H. St. John). This species seems intermediate between *P. oleracea* L. and *P. lutea* Sol. Further study of living material is needed to determine its position in relation to these two species.

LEUCAENA GLAUCA (L.) Benth. London, *Fosberg 12171, 13249* (BISH).

PHASEOLUS LATHYROIDES L. Paris, *Fosberg 13269* (BISH, USNA).

ABUTILON INDICUM Sweet. This shrub forms a conspicuous part of the vegetation near Four Brothers, *Fosberg 13215* (BISH, USNA). The species has previously been reported only from Jarvis and Baker Islands in the central Pacific. It is common in tropical Asia.

HIBISCUS TILIACEUS L. Paris, *Fosberg 13267* (BISH). Probably planted.

FALLS CHURCH, VIRGINIA

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 398–399 JULY, 1943

ANOTHER DRIFTLESS AREA ENDEMIC

NORMAN C. FASSETT

COMMELINA ERECTA L. var. **Greenei** Fassett, var. nov., foliis 10–15 cm. longis 6–8 mm. latis; spatheis maturis 1.5–2.7 cm. longis basi longe albido-villosis. WISCONSIN: on sand derived from crumbling sandstone, Cactus Bluff, 5 miles southwest of Sauk City, Sauk County, August 27, 1940, *J. T. Curtis & H. C. Greene* (TYPE in Herb. Univ. of Wisconsin); same station, July 7, 1941, *L. H. Shinners 3993;* same station, September 28, 1942, *N. C. Fassett & H. C. Greene 22056.*

This Driftless Area endemic (see Fassett, Rhodora **33**: 227, 228. 1931) has the size and proportions of var. *Deamiana* (Fernald, Rhodora **42**: 435–441. 1940) but differs in having long jointed white hairs on the spathe. Thus it bears the same morphological relation to var. *Deamiana* that f. *intercursa* Fernald does to var. *typica,* and that f. *crispa* (Wooton) Fernald does to var. *angustifolia* (Michx.) Fernald. It may, therefore, seem illogical to treat it as a variety when its counterparts are treated (and rightly) as forms. The reason is that while f. *intercursa* occurs as a sporadic variation throughout the range of var. *typica,* and f. *crispa* in like manner throughout the range of var. *angustifolia,* var. *Greenei* occupies a different area from that occupied by var. *Deamiana.* The latter occurs primarily in a limited range in northern Indiana[1] and northern Illinois, and has spathes always lacking white hairs more than 1 mm. long, as is evidenced by Fernald's statement based on his examination of the 16 collections cited by him, and corroborated by my own examination of the 16 sheets of this variety in the Deam Herbarium and the 6 in the Herbarium of the University of Wisconsin. That the plant of Cactus Bluff, isolated by some 200 miles from var. *Deamiana,* consistently has white-villous spathes is indicated by study of the 3 collections cited above; the last consists of 8 fruiting tops (all that could be found) collected for the purpose of studying the colony as a whole rather than a few individuals taken at random.

Var. *Greenei* occurs in very small numbers; Dr. Greene and I were able to find only 8 individuals. Such occurrence of rarities in extremely small numbers is quite characteristic of this part of Sauk County, which lies just within the Driftless Area. Only a few rods from the *Commelina,* on the steep face of Cactus Bluff, are a few individuals of *Pellaea atropurpurea,* known elsewhere in Wisconsin from two other bluffs, one a mile away and

[1] Mr. Deam has kindly loaned me his material of this group; the *C. angustifolia* of his Flora of Indiana (see pp. 285, 286, and Map 592) breaks clearly, in light of Fernald's treatment, into *C. erecta* var. *typica* in southern Indiana and var. *Deamiana* in northwestern Indiana.

the other 10 miles to the northwest. *P. atropurpurea,* primarily a southern plant isolated in the Driftless Area, occurs only in very small numbers, but *P. glabella* (Butters, Am. Fern Jour. **7**: 77–87. 1917), its common northern relative, is on nearly every cliff in southern Wisconsin (Tryon *et al.* The ferns and fern allies of Wisconsin, 23, 24. 1940). Mill Bluff, a mile and a half north of Cactus Bluff, was the type station for *Aconitum noveboracense* var. *quasiciliatum* (Fassett, Rhodora **31**: 49. 1929), where a very few individuals were seen (it is likely that it is extinct there now, since the woods shading the bluff have been cut). Fifteen miles to the northeast is Parfrey's Glen, where probably not more than a dozen individuals of the *Aconitum* cling to the moist shady walls of a ravine. Thirty miles northward, at Wisconsin Dells, *Rhododendron lapponicum* grows on cliffs along the Wisconsin River, at the only known station west of the Adirondack Mountains and south of Hudson Bay; it is doubtful if there are a score of individual plants at this place and their existence is menaced by the fact that the cliff on whose edge they grow is being cut back by the river faster than the newly exposed surfaces can be recolonized.

Surely many of the specialties of the Driftless Area are on the very brink of extinction.

DEPARTMENT OF BOTANY, UNIVERSITY OF WISCONSIN
MADISON, WISCONSIN

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 400–406 JULY, 1943

SUPPLEMENTARY NOTES ON AMERICAN MENISPERMACEAE—III

B. A. KRUKOFF AND H. N. MOLDENKE

New collections of the Menispermaceae, largely from Amazonian Brazil and Surinam, have recently become available to us. The Amazonian specimens were largely obtained in the municipality São Gabriel, State of Amazonas, on the tributaries of the upper Rio Negro, which are poorly known (to say the least) botanically. The collections were found to be of considerable interest and are discussed in the present paper. They extend our knowledge of certain species previously known from incomplete material; extensions of ranges are noted for a number of species, and three species are described as new. No changes in the nomenclature are necessitated.

The species are arranged in the same order and the place of deposit of specimens is shown by the same abbreviations as in our previous papers (1, 2, 3, 4). The following new abbreviation is used:

U: Georgetown Botanic Gardens at Georgetown, British Guiana.

CHONDODENDRON RUÍZ & PAVON

2. CHONDODENDRON PLATIPHYLLUM (A. St. Hil.) Miers. *Additional specimens examined: photos #34502* and *34501*.

As is evident from the labels (*photo #34502*), two specimens appear to be mounted on a single sheet, one collected by Casaretto in virgin forest in the State of Minas Geraes, and another collected by Richard near Rio de Janeiro.

Without seeing the actual specimen we are unable to ascertain whether or not *photo #34501* is of the type of *Cocculus ? cinerascens* A. St. Hil. The specimen was collected by Saint-Hilaire in forests near Rio de Janeiro.

3. CHONDODENDRON TOMENTOSUM Ruíz & Pav. *Additional specimens examined:* Peru, Ecuador, or Brazil, *collector undesignated 3, 10.* ECUADOR—NAPO-PASTAZA: basin of Rio Pastaza, *Gill 12363/6.*

On the labels of *collector undesignated 3* and *10* it is stated: "collected by Squibb's collector somewhere in Amazonian South America. Said to be a constituent of curare arrow-poison."

4. CHONDODENDRON CANDICANS (L. C. Rich.) Sandw. *Additional specimens examined:* BRITISH GUIANA—ESSEQUIBO: basin of Issororo River, *Jenman 5199* (U). Surinam—near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12305, 12335.*

It is satisfactory to have new collections of this species from Surinam. The species was known to us from Surinam only from the type collection of *Abuta ? Pullei.*

5. CHONDODENDRON LIMACIIFOLIUM (Diels) Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12090, 12092, 12093, 12095.*

7. CHONDODENDRON TOXICOFERUM (Wedd.) Krukoff & Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *? Froes 12087.*

SCIADOTENIA MIERS

3. SCIADOTENIA SOLIMOESANA Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS, basin of the upper Solimoes, *Froes 12094.*

This is the third collection of the species known to us.

ANOMOSPERMUM MIERS

1. ANOMOSPERMUM SCHOMBURGKII Miers. *Additional specimens examined:* BRITISH GUIANA—ESSEQUIBO: *Jenman 1333* (U); basin of Mazaruni River, *Jenman 2151* (U); Berbice: basin of Corentyne River, *Jenman 102* (U).

2. ANOMOSPERMUM DIELSIANUM Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12467.*

This is the first record of the species from the basin of Rio Negro (Corocoro on Rio Vaupes). It has been known hitherto only from the type collection from the basin of the upper Solimoes.

6. ANOMOSPERMUM CHLORANTHUM Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12113.*

This is the first record of the species from the basin of Rio Negro (Yuco on Rio Xie). The specimens are more pubescent than any of the previously examined and cited material.

7. ANOMOSPERMUM sp. nov. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12151.*

In a previous paper (1) we have given a description of a plant which presumably has never previously been described or named, but have not assigned a specific name to it in view of lack of flowers or fruits. The present collection is again sterile and from the same region as the two previous collections.

8. ANOMOSPERMUM BOLIVIANUM Krukoff & Moldenke. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12407.*

This sterile specimen matches very well the type collection of the species. It has been obtained in an old clearing on "terra firma" near Cucui.

9. **Anomospermum hirsutum** Krukoff & Moldenke, sp. nov. Frutex scandens; ramulis gracilibus dense hirsutis, pilis patentibus fulvis; petiolis gracilibus dense fulvo-hirsutis; laminis foliorum coriaceis late ellipticis argute acutis vel breviter acuminatis et saepe plusminus apiculatis integris subrevolutis, ad basim acutis indistincte 3-pli-nerviis, supra glabris nitidisque, subtus plusminus fulvo-hirsutis; costa venisque primariis secundariisque supra valde impressis, subtus argutiuscule prominentibus; reticulo venulorum copiosissimo perspicuo.

A woody vine; branchlets slender, densely hirsute on protected parts with spreading fulvous hairs 1–2 mm. long, less so or even glabrescent on the internodes; petioles slender, 2.5–3.8 cm. long, densely fulvous-hirsute, the uppermost 1 cm. swollen and usually more or less curved; leaf-blades coriaceous, uniformly bright-green on both surfaces or more shiny above, broadly elliptic, 7.5–16.5 cm. long, 2.5–6.8 cm. wide, sharply acute or short-acuminate and often more or less apiculate at apex, entire and slightly revolute along the margins in drying, acute at base, glabrous and shiny above, more or less fulvous-hirsute beneath, especially along the midrib and larger venation, indistinctly 3-pli-nerved from the base, the main pair of veins not very dissimilar to the 3 or 4 pairs of secondaries and confluent with them in many loops 6–8 mm. from the margins; midrib, principal veins, and secondaries rather deeply impressed above, sharply prominent beneath; the tertiaries prominulous in shallow grooves above, prominent beneath; veinlet reticulation very abundant and conspicuous under a hand-lens, fine, prominulous on both surfaces; only staminate flowers seen; pedicels subtended by 2 minute scale-like triangular-ovate to lanceolate bractlets, which are about 1 mm. long, carnose-thickened at base, acute at apex, hirsute on the back, and easily separable; sepals 6, imbricate, the 3 outer ones minute, resembling the bractlet, unequal, triangular-ovate, about 1.5 mm. long and 1 mm. wide, subacute at apex, sparsely hirsute dorsally and hirsute-ciliate on margins, carnose-thickened at base, easily separable, the 3 inner ones very much larger, broadly elliptic or suborbicular, narrowed and somewhat claw-like at base, rounded at apex, cucullate with inflexed margins, subequal, about 5 mm. long and 4 mm. wide, extremely carnose dorsally, glabrous, easily separable; petals 6, much smaller than the inner sepals, obpyramoid, about 2 mm. long and almost as wide, extremely carnose, the margins greatly inflexed, closely pressed together with the 6 stamens, forming a glabrous truncated "pseudodisk"; stamens 6, inflexed, when not extended equalling the petals and opposite them; filaments subterete or somewhat flattened, free, glabrous; anthers facing down and subhorizontal, dehiscing by short longitudinal slits; pistillate infructescences axillary, compound, to 9 cm. long, usually shorter than the subtending leaf, with about 3–12 fruiting-pedicels; peduncles obsolete; rachis slender, densely spreading fulvous-hirsute like the petioles and branchlets; bractlets linear, about 5 mm. long, densely fulvous-hirsute, one subtending each pedicel; pedicels slender, 1.3–1.8 cm. long, sparsely hirsute, 1–3-fruited, expanded-capitate at apex; mature fruits asymmetric, about 2.8 cm. long and 1.2–1.4 cm. wide, the exocarp slightly fleshy, glabrous, shiny, wrinkled in drying; mesocarp thin; endocarp hard and bony, smooth outside, elevated-reticulate within.

TYPE: *Ducke 753* (N), collected June 14, 1941, near "Manaos, Estrada do Paredão, silva secundaria non inundabili."

The species is unique and is immediately distinguished from all other known species of the genus *Anomospermum* as well as of the genera *Abuta, Chondodendron, Elissarrhena* and *Telitoxicum* by its hirsute leaves.

Specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Ducke 753* (N, type); *Froes 12408.*

TELITOXICUM MOLDENKE

3. TELITOXICUM INOPINATUM Moldenke. *Additional specimens examined:* BRITISH GUIANA—BERBICE: basin of Eberoabo River, *Hohenkirk 55* (U—iso-

type); Weruni-Ituni Savannahs, *Abraham 132* (U); basin of Courantyne River, *Hohenkirk 714* (U).

ABUTA BARRÈRE

2. ABUTA OBOVATA Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of Rio Negro, *Froes 12379, 12543, 12563.*

The species is now known both from the upper and the lower Rio Negro.

6. ABUTA PANURENSIS Eichl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Rio Negro, *Froes 12414.*

The species has been known hitherto only from the type collection. The present collection is from "restinga" near Yuco on Rio Xie, municipality São Gabriel.

8. ABUTA IMENE (Mart.) Eichl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12156;* basin of the upper Rio Negro, *Froes 12477.*

11. ABUTA GRANDIFOLIA (Mart.) Sandw. *Additional specimens examined:* VENEZUELA—AMAZONAS: basin of Rio Negro, *Froes 12387; Ducke 691.* BRAZIL—AMAZONAS: basin of Rio Tonantins, *Froes 12164, 12232.* SURINAM: near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12296, 12324.*

This is the first record of the species from the basin of Rio Tonantins.

14. ABUTA RUFESCENS Aubl. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12088, 12089, 12091;* basin of Rio Negro, *Ducke 861.* FRENCH GUIANA: *Aublet s.n.* (? type; photo #34499).

The Brazilian specimens are the first record of the species from the basin of Rio Solimoes.

15. ABUTA BARBATA Miers. *Additional specimens examined:* SURINAM: near Sectie O, on railroad Paramaribo-Dam, *Krukoff 12325.*

16. ABUTA GRISEBACHII Triana & Planch. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the Rio Negro, *Froes 12134; Ducke 822.*

20. **Abuta negroënsis** Krukoff & Moldenke, sp. nov. Frutex scandens; ramis crassiusculis adpresso-pubescentibus vel glabrescentibus; ramulis gracilibus densissime velutino-pubescentibus, pilis brevibus brunneis; cicatricibus perelevatis; petiolis crassis firmis ad basim ampliatis, dense velutino-pubescentibus; laminis foliorum coriaceis ovatis acuminatis integris, ad basim acutis vel paullo obtuseque subacuminatis, supra glabris nitidisque, subtus dense velutino-tomentosis, pinnato-venosis.

A woody vine; branches rather stout, about 1.5 cm. in diameter, appressed-pubescent or glabrescent in age; branchlets slender, very densely velutinous-pubescent with short brown hairs; leaf-scars large and corky, very prominently elevated on sterigmata about 5 mm. long; petioles stout, firm, 13–24 cm. long, ampliate at base, thickened and curvate for the upper 1.5–2 cm., densely velutinous-pubescent like the branchlets, the pubescence eventually wearing off; leaf-blades coriaceous, ovate, 25–37 cm. long, 14.5–20 cm. wide, acuminate at apex, entire, acute or very slightly obtuse-acuminate at base, glabrous and shiny above, densely velutinous-tomentose beneath with short, appressed, brownish hairs, pinnately veined; midrib stout, im-

pressed and often appressed-pubescent above, very prominent beneath; secondaries slender, 8–10 per side, regularly ascending, arcuate near the margins, usually not plainly anastomosing, impressed above, very prominent beneath; tertiaries slender, numerous, joining the secondaries, issuing at right angles, subparallel, slightly impressed above, prominent beneath; veinlet reticulation abundant and regular, forming very fine meshes visible under a hand-lens; flowers and fruit not known.

TYPE: *Froes 12423* (N), collected Dec. 19, 1941, near Santa Ana, on Rio Içana, basin of the upper Rio Negro, State of Amazonas, Brazil.

The species is unique and is immediately distinguished from all other known species of the genera *Chondodendron, Sciadotenia, Anomospermum, Abuta, Elissarrhena,* and *Telitoxicum* by the combination of the following characters: leaf-blades woolly beneath and distinctly pinnate-veined (not pli-nerved!). The only other known species of American menispermaceous plants which have the leaf-blades woolly beneath are *Abuta Grisebachii, Abuta Candollii, Abuta splendida, Sciadotenia paraënsis, Sciadotenia Sagotiana,* and species of *Chondodendron,* and leaves of all of these are pli-nerved.

All known species of *Chondodendron* are characterized by the matted indumentum whereas the leaves in our species are tomentose. Because of the absence of flowers, we cannot suggest its immediate relatives. It seems best placed in the genus *Abuta.*

21. **Abuta Froesii** Krukoff & Moldenke, sp. nov. Frutex scandens; ramis ramulisque gracilibus glabris nitidis; cicatricibus magnis elevatis circularibus suberosis; petiolis gracillimis glabris; laminis foliorum firme chartaceis ellipticis integris, ad apiceum rotundatis et cuspidato-acuminatis, ad basim rotundatis vel acutis, utrinque glabris pernitidisque, 5-pli-nerviis.

A woody vine; branches and branchlets slender, glabrous, shiny; lenticels usually prominent; leaf-scars large and elevated, corky, circular; petioles very slender, 2.5–7 cm. long, glabrous, somewhat ampliate at base, the uppermost 5 mm. thickened and curved; leaf-blades firmly chartaceous, uniformly colored on both surfaces, elliptic, 5.5–15.5 cm. long, 3–8 cm. wide, rounded to a short cuspidate-acuminate apex, entire, rounded or acute at base, glabrous and very shiny on both surfaces, 5-pli-nerved from the base; midrib and primary veins very slender, plane above, sharply prominent beneath; the lower pair of primary veins not as prominent as the upper pair, closely paralleling the leaf-margin half way to its apex, the upper pair not very arcuate, ascending almost to the apex, not anastomosing with the other pair nor with the secondaries; secondaries 1 or 2 pairs, in the upper half of the leaf, arcuately looped, not reaching the margins, anastomosing; tertiaries and veinlet reticulation obscure above, only the larger portions subprominulous beneath; flowers not seen; pistillate infructescences supra-axillary; peduncles stout, about 1 cm. long, subglabrous, surmounted by a large club-like receptacle, bearing (normally) three fruits; fruit asymmetric, 3–3.5 cm. long, 2–2.5 cm. wide, glabrous; exocarp hard and bony; mesocarp woody; endocarp thin, smooth and shiny, not corrugated.

TYPE: *Froes 12346* (N), collected Jan. 31, 1942, on "terra firma" near Macubeta on Rio Marie, basin of the upper Rio Negro.

The species resembles *Abuta brevifolia* from which it differs, however,

in its much larger fruits with the glabrous exocarp, much longer petioles, and larger leaves.

Specimens examined: BRAZIL—AMAZONAS: basin of Rio Negro, *Froes 12436;* basin of Rio Solimoes, *Froes 12168, 12180.*

ELISSARRHENA MIERS

1. ELISSARRHENA GRANDIFOLIA (Eichl.) Diels. *Additional specimens examined:* BRAZIL—AMAZONAS: basin of the upper Solimoes, *Froes 12084.*

THE NEW YORK BOTANICAL GARDEN
NEW YORK

Literature Cited

1. **Krukoff, B. A. & Moldenke, H. N.** Studies of American Menispermaceae, with special reference to species used in preparation of arrow-poisons. Brittonia 3: 1–74. 1938.
2. ————. A new name for *Cocculus toxicoferus* Wedd. Brittonia 3: 338. 1939.
3. ————. Supplementary notes on American Menispermaceae. Bull. Torrey Club 68: 237–243. 1941.
4. ————. Supplementary Notes on American Menispermaceae—II. Bull. Torrey Club 69: 156–161. 1942.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 406–417 JULY, 1943

WHAT IS THE TRINOMIAL TYPICUS?—II

LEON CROIZAT

The reader who has so far followed this discussion is aware by now of the sad plight of much nomenclature in our midst, and knows a few of the disruptive interpretations and peculiar ideas bearing upon the typic trinomial. This reader will agree, it may be believed, that a sane and constructive approach to the all-important problem of typification is impossible so long as the fundamentals in the issue are flouted, and the discussion wanders in a maze of pompous and ill-digested generalities. *Sharp and precise biological concepts such as necessarily underlie good classification cannot forever speak the language of fanciful nomenclature,* nor can the facts be concealed and disguised. It is no longer a question of names that are being published on occasion and prove untenable on account of some technical violation of the Rules, but of a whole deeply-rooted trend of unsound thought and haphazard practice, ultimately based on a lack of familiarity with the subject. The hair-splitting and the abuse of imagination which have characterized the work of some recent writers on nomenclature have damaged, no doubt, the cause of the serious student who is well aware that quibbling and wild hypothecating are as obnoxious in the long run as ignorance and neglect. At bottom, the Rules of Nomenclature are not a pack of cavil, the plaything of a few devotees, or the Book of Merlin. *They are a labor-saving device in the first place, making it possible for everybody to speak briefly and to the point on subjects of common interest.* Properly expounded, they are as easy to read and to understand as the rules governing any current card game. In a very definite sense, they must become a live reality to every botanist.

The fallacies surrounding the trinomial *typicus*, its nature and use, have no reason to exist, because this trinomial has nothing in it which is mysterious or difficult once its fundamentals are grasped. Rather than discuss these fundamentals in the abstract, I will deal with them by examples and plain considerations.

As an introduction, we may consider the following formula:

$$1 + x = 2;\ x = 2 - 1;\ x = 1.$$

Half a line of symbols and figures written in a matter of seconds speak an amount of truth which, put into words, would require considerable time and paper. The formula given above summarily states the following: A certain figure, conventionally designated by the symbol x, meaning a quantity unknown, when added to 1 yields 2. To find this figure transfer to the right of the symbol of equality the figure 1, changing its value from positive to negative, leaving x in its original position to the left of the sign of equality.

The result of the subtraction $(2-1)$ eventually yields 1, which is the value of x.

Precisely like mathematics, botany speaks in symbols and formulae, witness this: ***Hydriastele Kasesa*** (Laut.) Burret, comb. nov. = ***Ptychosperma Kasesa*** Laut. in Engl. Bot. Jahrb. **45**: 357. 1911. By the use of this formula, Burret (Notizbl. Bot. Gart. Berlin **13**: 484. 1937) tells his coworkers the following: "In a periodical called Engler's Botanische Jahrbücher, Volume 45, page 357, printed in 1911, Lauterbach has validly and legitimately published a certain species which he has designated as *Ptychosperma Kasesa.* I, Burret, having investigated the creation of Lauterbach, found in it characters which assimilate it to the species in the genus *Hydriastele.* Accordingly, I have brought Lauterbach's species away from *Ptychosperma* under *Hydriastele.* This of course, is my own, Burret's, understanding of the matter."

Obviously, it may not be doubted that botany, too, is ruled by a special kind of symbolic and abbreviated language. Nomenclature is essentially that branch of botany which is concerned with the proper use of such a language. The usefulness and nobility of nomenclature cannot be disputed or denied, for without it the use of this expeditious language would be impossible. Without this language, Burret would have been obliged to state its story in detail, that is, would have been forced back to the polynomial stage of botany and possibly farther still, to the age of Theophrastus and Pliny.

Let us now suppose that a taxonomist, J. Brown, is faced with the task of writing down the following account: In 1900 J. Doe published as *Planta una* an entity with a glabrous body and blue flowers. In 1905, P. Smith found a pubescent annual with blue flowers which he judged to be conspecific with *P. una* and published it trinomially, either as a subspecies or as a variety, as *P. una pilosa.* Five years later, in 1910, C. Black collected a pubescent herb with white flowers which he proposed as a form, *P. una albiflora.* Lastly, in 1915, N. Toe collected a glabrous herb with white flowers which he published as a form calling it *P. una leucantha.*

Using the standard language of botany, J. Brown has a free choice between two manners of expressing this long-drawn account. He can do this:

Planta una J. Doe, 1900.
P. una (subsp., var.) *pilosa* P. Smith, 1905.
P. una f. *leucantha* N. Toe, 1915.
P. una f. *albiflora* C. Black, 1910;

or this:

Planta una J. Doe 1900

P. una (subsp., var.) *typica* J. Brown, 1942.
P. una (subsp., var.) *pilosa* P. Smith, 1905.
P. una f. *leucantha* N. Toe, 1915.
P. una f. *albiflora* C. Black, 1910.

It will readily be seen that, while the two accounts substantially agree in the facts they reveal, the latter is in every respect better balanced. The

species itself is conceived as a broad unit, including both kind of plants, glabrous and pubescent, of which the glabrous entity is considered to be typical in the nomenclatural if not in the biological sense. The form *leucantha* spoken of as *P. una* var. *typica* f. *leucantha* is immediately known to be glabrous, therefore to belong to a complex other than the form *albiflora*. The trinomial *typica* neatly balances the trinomial *pilosa*, and a comparison between the type-specimens of the two can be effected without calling into question a binomial (*P. una*) and a trinomial (*P. una pilosa*) which may engender confusion. In brief: the segregation of the trinomial *typicus* has nothing about it which is mysterious, involved and philosophical; it is merely a book-keeping device which has for its result to simplify and elucidate the treatment of involved and much subdivided entities. This device is sprung into action by the simple expedient of publishing a trinomial (subspecies, variety or form) which is based upon the same type-specimen as the next higher unit; *P. una* and *P. una* var. *typica* being both based upon *J. Doe 482*, a specimen collected—let us say—near Washington, D. C., in 1899.

Some workers who are not familiar with this elementary device believe that *P. una* and *P. una* var. *typica* are synonyms, because—they say—"both these names apply to the same plant." This is a patent fallacy; to be synonymous (see Art. 16) two names must have the same *circumscription* (that is, be based upon specimens of the same significance and value in classification[2]), *position* (that is, be both under the same genus, species, variety, and the like), and *rank* (that is, be both genera, species, subspecies, varieties, or the like). It is clear that *P. una* and *P. una* var. *typica* cannot be synonyms, because they are short of two out of three elements required for a synonymy; they have the same *circumscription*, true enough, because they are both

[2] The term *circumscription*, etymologically considered, means to "write in" or to "delineate around," and is used by botanists in two senses, as follows: (a) To refer to groups in general. Accordingly, we hear that, for instance, "Exceedingly narrow circumscriptions were understood by Rafinesque to form good genera." (b) To define the taxonomic range of a specimen, as it were, thus: "*J. Doe 415* and *T. Brown 11* are collections with the same circumscription." It will readily be seen that the etymology of the term itself is compatible with these two different uses, and that both, consequently, are correct. However, the Rules speak of *circumscription* in the second sense only in the text of Art. 16. Users of the Rules should be careful not to understand the language of the Articles in the sense which is often colloquially current. A classic example of the confusion that results from misunderstanding the Rules in this manner, is Wheeler's contention (Contr. Gray Herb. 127: 53. 1939) that Watson published *Bernardia* (?) *fasciculata* as a *nomen provisorium* because he said that this name was ". . . only provisionally referred to *Bernardia*." That this notion is fantastic can readily be seen, considering that if Wheeler were correct every name published with an expression of doubt as to its true position or ultimate destination would be invalid. A *nomen provisorium* in the sense of the Rules (see Croizat, Jour. Arnold Arbor. 21: 499. 1940; 22: 137. 1941; Bull. Torrey Club 69: 454. 1942) is a very different thing. The rules must be read for what they are and must be used accordingly; no one should apply a monkey-wrench fitting the gear of a truck to the threads and screws of a fine microscope, for common sense forbids it.

based upon the very same specimen, but they do not have the same *position* (*P. una* stands under genus *Planta* while *P. una* var. *typica* stands under species *P. una*), nor the same *rank* (*P. una* is a species, *P. una* var. *typica* a variety).

The objection is sometimes heard that all these subtle distinctions among circumscriptions, positions, ranks and the like are quibbles, and that a botanist cannot be expected to waste his time nor to live by the codes of a lawyer. This objection must be buried once for all, for it sins against elementary reason. The difference between a competent and an incompetent worker is in the fact that the former has taken pains to learn to use all the instruments of his craft; meeting a difficulty, a straight-thinking student masters it once for all, and does not complain about it forever. The Treasury of the United States also makes some distinction between scraps of paper of the same size, texture and color, paying one-tenth as much for some of them, depending upon the fact that on these scraps the figure 1 is followed by one zero rather than by two. Strange to say, the supercilious and overbusy workers who dismiss circumscriptions, positions, and ranks with a sweeping and hopeless gesture of their hands are well informed of the "quibbles" of the Treasury, and never fail to exact their pound of flesh in good bills, squeezing the last drop of blood out of the Treasury's "legal notions." It is not very clear why these workers should dismiss as nonsense what the Rules of Nomenclature say, when, after all, they use taxonomic names fully as frequently as they do cash. True, profound treatises can be written about the conceptual background of x in mathematics, the theory of double entry in bookkeeping, the philosophy of the bad bridge player or of the shrewd "plunger" on the stock market, and about the nature of *typicus*. However, the average taxonomist has no need of all this literature to ply his trade well and intelligently. All that matters to him is to have a good grasp of the possibilities of the trinomial epithet *typicus* and of the brand of calisthenics which this epithet performs in actual use. It stands to reason that taxonomists who deal with complex entities or make a rigorous study of populations and variations need to use the trinomial *typicus*, and actually use it (see, for instance, St. John & Hosaka, Occ. Pap. Bishop Mus. **14**: 120. 1938; Clausen, Keck & Hiesey, Carnegio Inst. Wash. Publ. 520. 1940), while taxonomists who are fortunate enough to labor upon floras continuously yielding new species and possibly new genera have no feeling for this trinomial. The point is not that these are wise and those foolish, or the other way around. The point is, rather, that the practical necessities of the branch of taxonomy which these botanists serve call into play different means and methods, some playing the strings, others the brasses, in the orchestra of Flora. That all botanists should understand the needs of all botanists and be able on occasion to use all their tools is to be believed as a matter of course. It is none the less plain that since *typicus*

is meant to simplify, not to complicate matters, those who whip it into a froth of decorative generalities and ill-digested abstractions do not follow the middle of the road where alone common sense dwells.

A fallacy commonly heard about *typicus* is that this trinomial is a "new name." To begin with, this is denied by the Rules, for whenever they speak of a "renaming" or of a "new name" (see, for instance, Art. 61 and Art. 69), they refer to entities of the same rank, that is, to a species' acquiring a "new name" because an old and untenable binomial falls out, because a generic illegitimate name is replaced by another generic tenable unitarian designation, and the like. The Rules know better than to speak of a trinomial being given a binomial as a "new name." The Rules know, as a matter of fact, that to confuse ranks means to open the door to such errors as have been illustrated in the preceding discussion of Art. 58 and Art. 30.

The fact that the trinomial *typicus* cannot be a "new name" is conveniently illustrated by examples, this one, for instance: Mueller Argoviensis published *Mallotus oreophilus* (in DC. Prodr. **15**(2): 964. 1866) without ending the specific description with the designation of a type-specimen. At the same time, however, he published two trinomials, *α ochraceo-albidus* and *β floccosus,* typifying the former by a specimen with whitish-tomentose, the latter by one with glabrescent leaves. Of these trinomials the former, designated by the letter *α* is the full equivalent of a trinomial *typicus* because its type-specimen is also the type-specimen of the binomial.

Translated into plain language, Mueller's publication means that he recognized an entity (the species, *M. oreophilus* in the broad sense) with general characters of fruit, flower and the like that applied in common to the subdivisions of this entity (the varieties, distinct in the nature of their indumentum at the leaf), one of these subdivisions being accepted by him as typic of the species as a whole *in the nomenclatural sense, not necessarily in the biological one.* It should not occur to a competent biologist and to a well informed taxonomist that the concepts involved in this treatment are two, for they are manifestly three, namely: (1) a broad aggregate of forms, whitish-pubescent to glabrescent in their foliage, but akin in the balance of their characters (*M. oreophilus*); (2) a subdivision of this aggregate with definitely whitish-pubescent leaves, this character in Mueller's opinion setting out a morphological and possibly a geographical complex (*α ochraceo-albidus*); (3) a subdivision like the preceding one but glabrescent in its foliage (*β floccosus*). Since the concepts here involved are three, not two, that bearing upon *M. oreophilus* in particular being unlike that of *α ochraceo-albidus*, it stands to reason that this trinomial cannot be, and is not a "new name" for the binomial. It is a *different name, for it applies to a different subject and holds within itself a different concept.* To designate *M. oreophilus α ochraceo-albidus* as a "new name" violence must be done to the whole

of the Rules which define as such something different. It is not clear in my understanding why such a violence should be done, when it leads only to ultimate confusion of terms and concepts, and serves no useful purpose at all. What does a taxonomist gain who follows the typic trinomial with the abbreviation "nom. nov." rather than with the accepted "var. nov." or "subsp. nov."? Does he affirm in so doing his faith in the esoteric side of nomenclature, proclaiming unto the ages his perfect understanding of the virtues of *typicus?* Indeed not: he merely states that his familiarity with the concepts underlying such a trinomial is less perfect than it ought to be, and confuses his coworkers by palming off as a "new name" of undefined status that which is clearly not so.

Some objection may be anticipated against my using in this summary two examples which are seemingly different without emphasizing this presumed difference. It may be pointed out that in the fancied case of *Planta una* J. Doe, 1900, the typic trinomial was segregated only in 1942 by a taxonomist other than J. Doe, namely J. Brown, while in the actual case of *Mallotus oreophilus,* Mueller himself immediately segregated the trinomial in question and a second one, failing to designate the type-specimen of the binomial.

No difference at all *in concepts* exist between these two examples. Proof of this is immediately had by comparing the examples I have used in their basic final form. Here they are:

(A) *Planta una* J. Doe, 1900.

P. una var. *typica* J. Brown, 1942. *P. una* var. *pilosa* P. Smith, 1905.

(B) *Mallotus oreophilus* Muell.-Arg., 1866.

M. oreophilus var. *ochraçeo-albidus* Muell.-Arg., 1866. *M. oreophilus* var. *floccosus* Muell.-Arg., 1866.

Nothing would change in the realities involved by these citations if J. Doe himself had published var. *typica* in 1900, or if Mueller had waited half a century to announce var. *ochraceo-albidus.* Both *P. una* and *M. oreophilus* ultimately have acquired the conceptual status of the species in the broad sense, that is, of the biological complex as a whole. Their trinomials *typica* and *ochraceo-albidus* have exactly the same significance, that is, they stand for the part of the species broadly understood which is typic in the nomenclatural sense. Likewise, the subdivisions *pilosa* and *floccosus* are equivalent in this, that they represent a nomenclaturally atypic segment of the binomial. Clearly, the var. *typica* (1942) of *P. una* (1900) is no more a "new name" of the binomial than is the var. *ochraceo-albidus* (1866) of *M. oreophilus* (1866). Precisely in the same manner, two bars of iron of the same length and weight are identical regardless of the fact that one was sawed off the mother bar in 1866, the other in 1942.

The fallacies current on account of failure to properly understand the elements of time and concept in nomenclature are so numerous that I may add parenthetically a few words on the subject. As I have shown, Art. 18 pitilessly scrambles three "types," namely (1) type-names; (2) type-specimens; (3) biological types; falling as a result into the grossest contradiction. I have good reason to suspect that such unfortunate results are chargeable, more than to anything else, to a single factor. The near totality of taxonomists untrained in the use of *typicus* and trinomials in general overstress the element of time against the element of concept. Accordingly, they are panicky or rebellious when somebody speaks of the trinomial *typicus* as the "type" of the species. They cannot see this at all, for they point out that a species must have a "type," and that it is not true that all species have a trinomial *typicus*. Naturally, they argue, the "type" must be a specimen, figure, or description, for without such a "type" a species cannot even be born. A species, they further argue, does not need a trinomial *typicus* to be born.

Instead of turning obdurate or panicky, these taxonomists ought to consider that they can publish *Planta una* in two manners, (1) by designating the type-specimen and adding no trinomial, as follows: *Planta una*—type-specimen: *J. Doe 372.* (2) By designating the type-variety together with some other trinomial (in theory, the type-variety alone could be legitimately and validly published, nothing forbidding this in the Rules) and listing the specimen either after the binomial or after the typic trinomial, as follows: (a) *P. una*—type-specimen: *J. Doe 372;* var. *typica* (*una, genuina,* etc.); var. *lutea;* (b) *P. una;* var. *typica*—type-specimen: *J. Doe 372;* var. *lutea.*

It is for all to see that in the publication of *P. una* two elements are involved or may be involved, namely, (1) a type-specimen; (2) a type-variety. It is just as clear that the type-specimen may not be designated at publication, and so may not be indicated the type-variety. It is downright untrue, of course, that a species needs the designation of a type-specimen to be born. The species of older authors, as a matter of fact, were practically all published without mention of specimens, least of all of type-specimens. Naturally, it is just as feasible to publish a type-variety without designating a type-specimen, as it is to designate a type-specimen without publishing a type-variety. To elucidate this vital point, let us suppose that *Planta una* was published in 1801 in a valid and legitimate manner, without, however, the indication of a type-specimen or of a typic trinomial. It is open to a modern worker to choose right now this specimen and to publish this trinomial. Conversely, the type-specimen might have been chosen by a taxonomist in 1825 and the type-trinomial (var. *typicus, genuinus* and the like) published by another taxonomist in 1930. In other words: *the concept of type-specimen (or its equivalents, description and figure) and the concept*

of type-name (trinomial typicus or its equivalents) are both hidden within the entrails of the species at birth and no limitations in time exist—in principle—to their being pulled out to light. The taxonomists of an earlier generation were inclined to muster into the world the type-trinomial sooner than the type-specimen, thus publishing a var. *typica* or the like even before having designated the type-specimen; we moderns, on the contrary, not only incline to bring forth the type-specimen first, but go so far as to accept our point of view as the whole truth, denying that a typic trinomial and a type-name in general is a "type" at all. This is an error, and so long as this error lives we will be unable to progress in nomenclature, for nomenclature is the art of putting together right names and right specimens. Obviously, to fit these entities together well we should be able to effect at all times and under all circumstances the proper distinction, what is a name and what is a specimen. Somebody who was not innocent of nomenclatural affairs wrote in Rec. iv of the current Rules the statement that the type of a new name in a species is "the type-variety or specimen." Another somebody who was well advanced in knowledge, taking it for granted that sooner or later every species is bound to have a type-trinomial, spoke in Rec. xviii of the "subdivision of a species" which is "the type of the specific name." Since Art. 18, the ark in which is supposedly embalmed the "Type Method" itself, emphatically states that the type of a species is only a specimen, description or figure—as already pointed out—the reader may draw his own conclusions as to the happy state of affairs that now prevails, with two Recommendations which contradict a "fundamental" Article which contradicts itself.

Still another fallacy current on the score of *typicus* and its nomenclatural equivalents is the belief that these epithets have hidden virtues of their own, which set them apart from the common run of other taxonomic names. At the very end of the paper of Bolle elsewhere discussed in this review, Harms, Mattfeld, and Pilger contend that Bolle is wrong in his approach to the trinomial *typicus*, "da nach unserer Meinung diese Ausdrücke nach dem Sinne der Regeln nicht den eigentlichen Epitheta gleichzusetzen sind, vielmehr nur als Bezeichnungen fur eine Untergruppe gelten sollen, die dem Typus der übergeordneten Gruppe entspricht" (in our view, these terms—*typicus, genuinus,* etc.—cannot be assimilated to true epithets in the sense of the Rules, because they are mere symbols for subordinate units which contain the type of the higher ones).

On its face, this statement seems to be salted with philosophical flavor. Its authors draw a distinction between "Epitheta" and "Bezeichnungen," inferring that Bolle is at fault because he failed to perceive how substantially different are these two objects of nomenclatural thought, the "Epitheta" and the "Bezeichnungen." Had Bolle seen this radical difference, we are led to understand, he would not have written a paper at all to ask that

a Recommendation be enacted to check the spread of the use of *typicus, genuinus*, and the like trinomial epithets. Bolle would have worshipped the "Bezeichnungen" and the "Epitheta" at different shrines, as do his censors, and abstained from sacrilegious writing.

I do not believe that Bolle is right, as the reader knows, but I believe even less that his critics have a plausible case on their hands. The statement that *typicus* and its kindred are "Bezeichnungen" not "Epitheta" has mystical flavor much rather than philosophical taste. Like all mystical affirmations, this *pronunciamento* appeals to the heart of those who happen to accept it on faith, but cannot appeal to the mind of a dispassionate investigator. Once again, this is a saying which is rooted in something taken for granted rather than carefully digested. What amount of thought do I convey to myself and others when I utter the jaculatory: "The typic trinomial is not an epithet but a symbol (Bezeichnung)"? The answer is that I mean nothing at all. Every word, written or spoken, is both an epithet and a symbol of something that exists in nature or in the mind of man. Properly juggled, the letters a, e, r, t, and w spell *water* which is both the name (epithet) and the connotation (symbol) of a fluid that can be drank, swum through, and navigated on. So juggled, other letters can be made to spell *Cabralea macrantha* Harms, which is the name for a certain meliaceous plant from Rio de Janeiro, and the symbol of this entity in the eyes of a botanist, who by reading the name can visualize the plant. Still other letters suitably combined read *Croton scaber* Willd. var. *genuinus* Muell.-Arg., which is both the name and the "Bezeichnung" for a group under *C. scaber* which, being typic in the nomenclatural sense, if not in the biological one, cannot be segregated from *C. scaber*. Is there any difference between such a "Bezeichnung" as *C. macrantha* and such another as *C. scaber genuinus*? None indeed that can be seen; both apply to certain plants which they symbolize before the eye of a taxonomist. True, a binomial is not a trinomial and a *Cabralea* is not a *Croton*, nor is a typic variety an atypic one, even as stale bread is not fresh bread, but the names of all these quantities are "Bezeichnungen" in their own right, and it is not what they are in the abstract that counts but *how they react when used*. How do Harms, Mattfeld, and Pilger factually differ from Bolle in regard to handling the trinomial, *typicus* or like epithets? So far as it may be gathered, only in their belief that these names are "Bezeichnungen" while Bolle takes them for "Epitheta," a difference which, as it has been shown, rests on the false assumption that a fundamental distinction is established between the two. What is then the *practical* implication of what the three authors write? None that these authors are able to state, beyond uttering the dictum that the proposal to drop *typicus* in the future is useful but not necessary ("ist zwar nützlich, aber nicht erforderlich"). How useful and to what extent neces-

sary, or the other way around, and why, Harms, Mattfeld and Pilger, do not say. The affectation of brevity and pointedness displayed by oracular statements which are not short because they call for controversy, nor pointed because they miss the vitals of an issue, invites Montaigne's comment, as quoted by the elder De Candolle (Théor. Elem. Bot. 310. 1819): "C'est dommage que les gens d'entendement aiment tant la briéveté; sans doute leur réputation en vaut mieux, mais nous en valons moins." (It is a pity that those-in-the-know so like to be brief; no doubt, their fame soars on this account, but we of the common people are left in the lurch.)

In affirming that *typicus* is a "Bezeichnung" in the sense of the Rules ("nach dem Sinne der Regeln") Bolle's opponents appeal to the Rules as if they contain Articles or Recommendations to favor such an appeal. The Rules, in fact, reject it. Article 8 states: "Nomenclature deals with: (1) the *terms* which denote the rank of taxonomic groups (Art. 10–14); (2) the *names* which are applied to the individual groups (Art. 15–72)." In the German text of the Rules the word *terms* is rendered as *Fachausdrücke* (which is clearer, if possible, than its English counterpart), the *names* being known therein as *Namen*. Not a word is said about "Bezeichnungen" of any kind, and Art. 8 leaves no room to quibble, for it specifies the numbers of the Articles which deal with *terms* as against those dealing with *names*. Since the trinomial *typicus* and its equivalents are mentioned for the first time by implication in Art. 18 and Rec. iv, and openly by Rec. xviii following Art. 30, it is patent that this trinomial and its kindred are *names* according to the Rules. They differ, as we have seen, from other names only in one respect; they cannot be transferred unless they are accompanied by the units which they typify. *This is not so much because they have special virtues of their own, and are "Bezeichnungen" rather than "Epitheta," as because certain epithets normally used to connote the type-units below the binomial lend themselves to ambiguity when they are thoughtlessly transferred.* Proof of this statement is in the fact that *Acomastylis elata* var. *genuina* and *A. elata* var. *elata* have the same meaning in taxonomy and the same function in nomenclature; they are absolute synonyms, as a matter of fact, because (see Art. 16) they have the same position (both stand under the same species, *A. elata*) the same circumscription (both are based upon the very same type-specimen), and the same rank (both are varieties). The only difference between these Siamese twins is a matter of detail: *A. elata* var. *elata* can be transferred as easily as any other trinomial—despite its being a "Bezeichnung," not an "Epitheton," if we are to believe certain expounders—while *A. elata* var. *genuina* cannot be transferred without loss of meaning on account of the general nature of the epithets *genuinus* and *typicus*. That a detail, not an essential point is here involved can be further proved by reference to the fact that a taxonomist who intends to publish the

typic variety of *A. elata* is perfectly free to use *genuina* rather than *elata*, or the other way around. He may use either one with the assurance that he will state precisely the same thing, convey the same meaning, be understood in the same sense. That so trifling a difference between *genuina* and *elata*, or any other such set of trinomials, should have engendered lasting confusion, called for a monumental outpour of platitudes, ill-digested notions and loose thought, is truly astounding.

It may be asked whether it is convenient to retain *typicus, genuinus* and the like in view of the positive liability which these epithets carry in their bosom when transferred. My opinion is that we must put up with these trinomials because they are already in the record, and it proves impossible to outlaw them without inflicting irreparable damages upon the nomenclature now accepted. Nor is this liability without its compensation, for there is no opportunity for mistaking any trinomial labelled *typicus, genuinus,* or the like for a trinomial lacking typic status. As my final thought on the matter, I state my belief that the proper way of dealing with a delicate and exacting piece of machinery is not hitting it with a sledge-hammer, but learning how to use it. A student who intends to prepare himself for botanical work must put up with *typicus* and be ready to master its intricacies, precisely as he must learn to match specimens and to write a tolerable Latin diagnosis, all these being the essential requirements of his craft. Once the proper functions and the correct use of *typicus* are understood and suitable amendments are introduced into the Rules by those who understand these functions and this use, all reasons fall for preferring *typicus* to another trinomial.

As a matter of fact, even under the Rules now in vigor such trinomials as *Acomastylis elata* var. *genuina* must be transferred to *A. Peckii* as *A. Peckii* var. *elata,* not as *A. Peckii* var. *genuina,* for the following reason:

(1) Article 18 states that the nomenclatural type is *permanently* attached to the group which it typifies. True, Art. 18 states at the same breath that the nomenclatural type of a species is a specimen, figure or description. This, however, is belied by the very *Note* in Art. 18 and by Rec. iv and Rec. xviii.

(2) Article 55 orders that the earlier valid epithet must be transferred when a trinomial is moved from one species to the other. This order contradicts the very definition of nomenclatural type given by Art. 18. Accordingly, Art. 18, Art. 55, Rec. iv and Rec. xviii work at cross purposes.

(3) Article 5 states that in the absence of a relevant rule, or when the consequences of rules are doubtful, established custom must be followed.

(4) "Established custom" cannot conflict with Art. 4 which prescribes that forms and names which may cause error and ambiguity or throw science into confusion must be rejected.

In conclusion, since it is patent that *Acomastylis elata* var. *genuina* when transferred to *A. Peckii* as *A. Peckii* var. *genuina* yields a citation which causes error and ambiguity and throws nomenclature into confusion; that the consequences of the Rules are doubtful in the case at hand; that established custom must be followed; that established custom cannot tolerate forms that cause error and ambiguity;—it follows that *A. elata* var. *genuina* must be transferred to *A. Peckii* as *A. Peckii* var. *elata*, because this transfer (a) is factually correct in not altering the typification by specimens in the least; (b) is unequivocal, once the basinym is given and suitable critical notes are furnished. Naturally, no one should forever be expected to reconstruct the Rules where the Rules have broken down, as they have in the present case. Accordingly, the Rules must be suitably modified to take care of the contingencies illustrated in this discussion. However, to sum up, even under the present Rules it is possible to effect the proper transfer of the trinomial *typicus*, as has been shown.

SUMMARY

Two proposals made to amend the existing Rules of International Nomenclature in regard to the typic trinomial (subspecific group *typicus*, *genuinus*, and the like) are discussed in detail, reaching the conclusion that these proposals are unacceptable. The belief that the trinomial *typicus* differs from other trinomials in essential characters is refuted, and it is shown that the segregation of such a trinomial does not constitute a "new name." In the face of widely circulated misapprehensions the true meaning of Art. 30 and Art. 58 of the current Rules is reestablished. To take care of the inconveniences arising when the trinomial *typicus* is transferred, a modification is proposed to Art. 55, showing at the same time that Art. 18 on the so-called "type method" is shot through with contradictions both in the text and in regard to Rec. iv and Rec. xviii of the current Rules. A brief account is given, based on examples, of the nature and function of the typic trinomial. It is shown how this trinomial can be properly transferred even under the existing imperfect Rules.

ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 4, pp. 418–429 JULY, 1943

THE STATUS OF CERTAIN ANOMALOUS NATIVE CRAB-APPLES IN EASTERN UNITED STATES

ROGERS MCVAUGH

Well known to anyone who has grown apples from seed is the abandon with which these plants produce viable and fertile hybrid offspring. Intervarietal and interspecific crosses are produced freely, not only among apples but among species of most of the related genera. The several genera of the apple family (or subfamily) have long been noted for this behavior, and much of the distress felt by earnest taxonomic workers in this and other rosaceous groups is traceable directly to it. The combination and recombination of characters brought about by repeated crossing, coupled with the chromosomal irregularities which are often initiated by such hybridization, has made the positive segregation of genetically distinct species almost impossible in certain populations.

In view of this tendency toward hybridization, it is not surprising to find that fertile crosses can be produced between the common cultivated apple on the one hand, and the native American crabapples on the other. There has been little concerted effort to effect experimental crosses of this sort except with stocks of the prairie crab, *Malus ioensis* (Wood) Britton; this one species has been the subject of extensive investigations, chiefly by Professor N. E. Hansen of South Dakota, and some desirable new hardy hybrid stocks and varieties have been produced.[1] Native crabapples are common, however, in eastern United States, especially along the mountain chains from western New York to Alabama and Georgia, and there would appear to have been ample opportunity for cross-fertilization in this region, where the cultivated apple has flourished since its first introduction by the early colonists.

As Professor L. H. Bailey has recently pointed out[2] in connection with his own studies of the blackberries, it is neither safe nor scientifically sound to assume hybridity for puzzling forms which do not fit one's conception of any known species. The principal criteria of hybridity, as he goes on to say, are mostly three in number: "(1) presence of the two [supposed] parents in the vicinity; (2) occurrence usually in small numbers, as if incidental or exceptional to the main population; (3) characters that appear to belong only to the parents in various degrees of combination." Actual proof of hybridity, of course, is sometimes possible by means of self-pollination (or at

[1] See, for example, the following by Professor Hansen: Plant Introductions (1895–1927). So. Dak. Exp. Sta. Bull. 224: 1–64. 1927; ibid. 309: 1–16. 1937; New Hardy Fruits for the Northwest. ibid. 339: 1–31. 1940; Taming the Native American Apple. Rep. So. Dak. Hort. Soc. 36: 61–62. 1940.

[2] Gentes Herb. 5: 7. 1941.

least controlled pollination) of suspected hybrids; hybrid seedlings from continued crosses will eventually reproduce in some measure the combinations of characters found in the original species. Controlled crossing experiments are not always possible, however, especially with woody plants which take several years to come to maturity, so that the student must often content himself with observations on the plants as they occur in nature.

Recently I have had occasion to collect and study material of the native crabapples, and my attention has been focused from time to time upon certain trees which are atypical—trees which appear to be anomalous in the midst of the general population. These peculiar trees, occurring at widely separated localities from Delaware to Georgia and west to Indiana, look at first glance like crabapples which are but a little out of the ordinary. The technical characters are, for the most part, those of the American crabapples, so that any demonstration of their hybrid origin must rest upon their less obvious and perhaps intangible features. The most obvious difference between these nonconformists and the ordinary native crabapple is that in the latter the leaves of vigorous shoots, and sometimes those of the fruit-spurs as well, are provided with broad sharp lobes, so that the blades sometimes simulate those of the red maple. In the aberrant individuals, on the other hand, the blades are less strongly or not at all lobed, and so sometimes resemble those of cultivated apples.

In 1913 Professor Alfred Rehder designated as a new species *Malus platycarpa*, a native crabapple in which the leaves were said to be "oval or elliptic, acute, serrate, not lobed, or sometimes slightly lobed at the end of vigorous shoots." Thus was unwittingly created a convenient repository for any native crabapple with unlobed or slightly lobed leaves; botanists since 1913 have availed themselves of this to such an extent that the name *Malus platycarpa* has lost its specific application and is now used for a whole series of forms which appear to be of hybrid origin. We need not pass here upon the genetic constitution of Rehder's original material, but his description, as will be pointed out below, sounds peculiarly like that of one of our suspected hybrids.

The following table contrasts briefly the more obvious features of the cultivated apple with equivalent ones pertaining to the American crabapples of the Section *Chloromeles* (Decne.) Rehder;[3] the latter are considered as a

[3] It should be noted that if the name Sect. *Chloromeles* be used for the group of the American crabapples, it then becomes necessary to revive Sect. *Calycomeles* Koehne (Deutsch. Dendr. 257. 1893) for the group called by Rehder Sect. *Eumalus* Zabel. Koehne's Section *Calycomeles* originally comprised all the species of *Malus* supposed by him to have a persistent calyx, including the American species *M. coronaria* and *M. angustifolia*, five Old World species having involute unlobed leaves (now referred by Rehder to *Eumalus*), and *M. "crataegifolia"* (*M. florentina* (Zuccag.) Schneid.), now referred by Rehder to a subsection of Sect. *Sorbomalus*. This latter species was apparently included in *Calycomeles* by an oversight or error, since according to Schneider and Rehder it has a deciduous calyx.

unit, the several species agreeing closely in technical characters. Also contrasted below are the characters of the series of plants called *Malus platycarpa*, including not only the original *platycarpa* of Rehder, but also certain other native plants, referred to above, which have various features in common.

A Cultivated Apple	B "*Malus platycarpa*"	C Other American Crabs of Section *Chloromeles*
Trunk becoming thick in age, often more than 30 cm. in diameter.	Trunk reaching a maximum diameter of at least 35 cm.	Trunk usually 15 cm. in diameter or less, sometimes reaching 25 cm.
Branches not thorny.	Branches thorny or in some plants not at all so.	Branches usually definitely thorny.
Leaves rolled (involute) in the bud.	Leaves folded (conduplicate) in the bud	
Leaves never lobed normally, even on vigorous shoots.	Leaves usually unlobed, or those of vigorous shoots lobed.	Leaves regularly lobed, or those of the fruit-spurs unlobed.
Fruits various in size, often 5–10 cm. in diameter.	Fruit often 4–6 cm. in diameter.	Fruit usually not more than 4 cm. in diameter.
Fruit usually red or yellow, or red-cheeked.	Fruit green, yellow, or red-cheeked.	Fruit green, yellowish-green or yellow.
Fruit with a small depression at apex, the core united with the flesh and its apex not protruding.	Core with a free pointed apex not fused with the flesh of the fruit.	
Pedicels short and stout, usually 1–2.5 cm. long, and up to 2 mm. in diameter.	Pedicels nearly like those of group C, but sometimes shorter and stouter.	Pedicels slender, often 3–4 cm. long, about 1 mm. in diameter (exceptions in Ohio–Indiana region and w.)
Pedicels and outer surface of hypanthium densely pubescent at flowering time.	Pedicels and hypanthium usually pubescent, sometimes densely so.	Pedicels and outer surface of hypanthium glabrous (exceptions as above and pedicels sometimes sparsely pilose).
Anthers pale yellow.	Anthers pink or salmon color, or yellow with almost no pink.	Anthers pink or salmon-color.
Flowering season early.	Flowering season that of group A or slightly later.	Flowering season late.

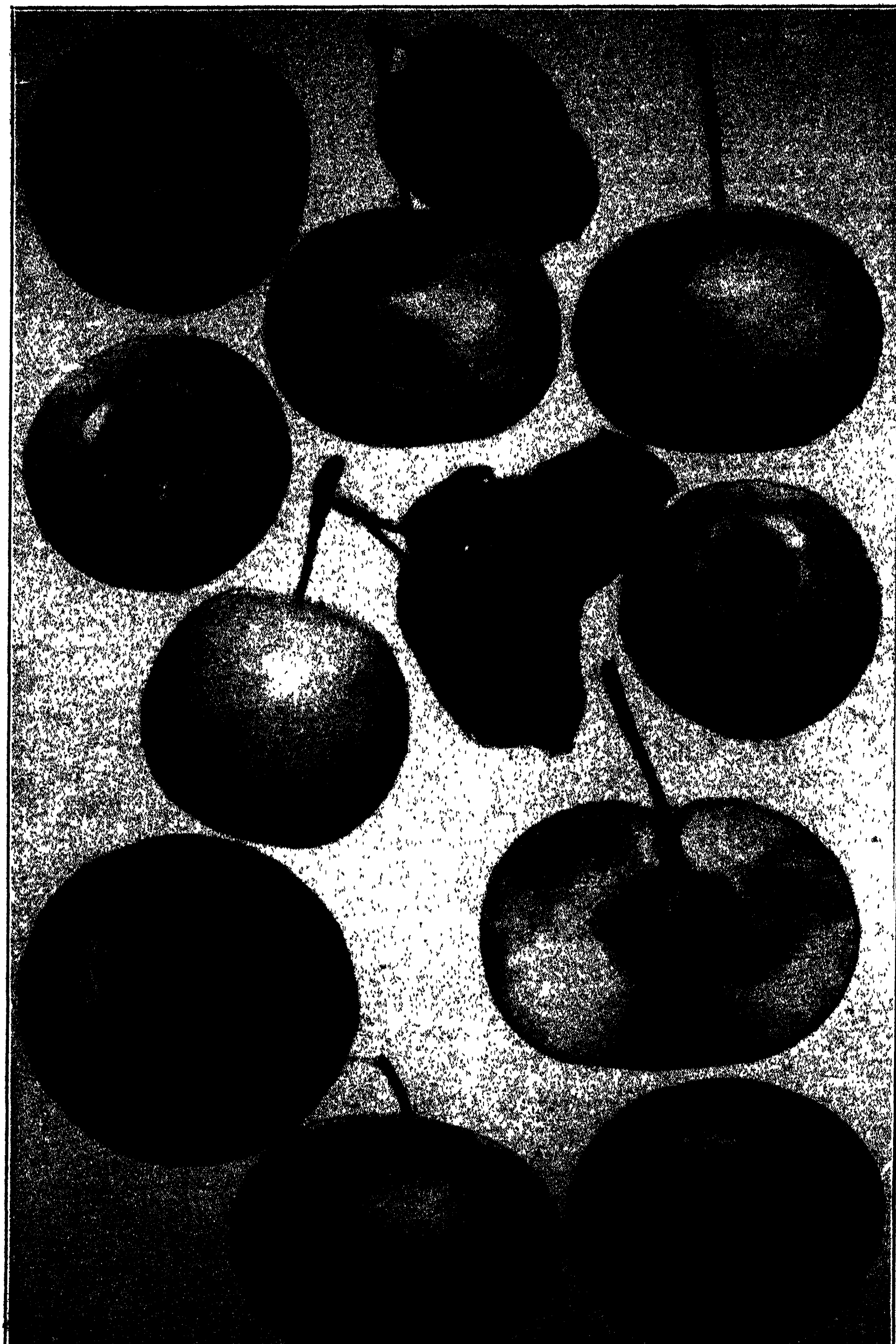
It is at once evident, upon inspection of the table, that the "*platycarpa*" group is morphologically intermediate between the American crabs and the cultivated varieties, showing an undoubted affinity to the former. Professor Bailey's third criterion of hybridity, the appearance in the supposed hybrid of characters belonging to the two parents, may be abundantly tested with

The section *Calycomeles* may accordingly be typified by one of the remaining species. Since Rehder has already typified his section *Chloromeles*, basing it upon *Malus angustifolia* (Jour. Arnold Arb. 2: 49. 1920), there is left in *Calycomeles* a group of species all of which have been included by recent authors in *Eumalus*. Since *Calycomeles* (1893) antedates *Eumalus* (1906) it is necessary to employ the former when using it as the name of a section. The Section *Calycomeles* may be typified by *Malus sylvestris* Mill.

respect to *Malus platycarpa*. Many of the characters of the American crabs appear to be wholly or partially dominant, so that all the supposed hybrids which I have seen resemble these species rather markedly. In this connection it is noteworthy that crabapples of known hybrid ancestry, specifically a series of the Hansen hybrids between forms of *Malus ioensis* and varieties of the cultivated apple, resemble the former very strongly. A series of these hybrids is available for study at the U. S. Plant Introduction Garden at Glenn Dale, Maryland; in all characters of leaves and branchlets they are strikingly similar to the *ioensis* parent.

Although trees of the supposed "*platycarpa*" stock have certain features in common, the stock is by no means a homogeneous one. Trees from different localities differ markedly in characters of the branches (chiefly in the greater or lesser number of thornlike branchlets present), in leaf-shape, and in size and other characters of the fruit. The fruits of "*platycarpa*," while usually larger than those of the native crabapples, are as variable as might be expected among the offspring of the hundreds of varieties of cultivated apples. They vary in shape from flat or depressed-globose (the shape of the original *platycarpa*) to globose (sometimes even becoming higher than broad); one tree near Andrews, North Carolina, bears apples of a sheep-nose type. In color these fruits vary from a dull green like that of some native crabs to a clear pale yellow not unlike that of the Transparent, or to a red-cheeked form resembling some of the cultivated crabapples. It seems altogether improbable that fruits of such diverse types should be produced by a single species, especially since no other native species is known to vary in this way, and it seems probable that the different sorts have arisen following hybridization between native apples and cultivated varieties which are distinguished chiefly by fruit-characters (figs. 1, 2).

In almost all the other characters which are readily studied, plants of *Malus* "*platycarpa*" resemble the American apples rather than the European one; it is even possible, moreover, to suggest which of several species of native crabs may have been concerned in the supposed cross, chiefly through study of leaf-characters. In the region where *Malus angustifolia* is the only native apple, the southeastern Coastal Plain and Piedmont, the leaves of "*platycarpa*" invariably approach those of *angustifolia* in shape and petiole-length; between Baltimore and Wilmington, however, where several colonies of "*platycarpa*" are known, the leaf-shape and petiole-length of these plants approach that of *M. coronaria*, the prevailing species of that region (see figure 3). In areas like that in the vicinity of Asheville, North Carolina, where both *M. angustifolia* and *M. coronaria* and its relatives occur, it has not been possible to distinguish between the effects of the two species in crosses with cultivated varieties.



A character which is doubtless related to the genetic constitution of any given plant, but which is not readily evaluated except by comparative and simultaneous studies on whole series of plants, is that of date of flowering. This date is influenced to a considerable extent by regional and local climates and by other factors, and so varies somewhat from place to place and from year to year. Different species and varieties of apples, however, appear to bear a reasonably constant relation to each other in this respect. Where *Malus glabrata, M. coronaria,* and *M. angustifolia* grow together, the flowering period of the first two is a week or ten days ahead of that of *M. angustifolia,* and is slightly preceded in its turn by the flowering of the cultivated apples. This relation appears to obtain regardless of season or locality. One would expect, therefore, that hybrids of *Malus angustifolia* would be met with infrequently, because of the rather considerable discrepancy between its flowering period and that of the cultivated stock. This is borne out in practice, so far as I have observed; most of the plants of "*platycarpa*" have been found in areas where *M. coronaria* is the only native species known to occur. *Malus glabrata* is not taken into consideration, as it is a rare species confined to high coves in the mountains of western North Carolina.

Plants of *Malus* "*platycarpa*" regularly flower with or slightly later than cultivated apples in the same vicinity, and considerably ahead of plants of *M. angustifolia,* but precede *M. coronaria* not more than a few days. In the vicinity of Washington, D. C., on April 19, 1942, thickets of "*platycarpa*" apples were budding, with pink-balloon-like petals just beginning to separate; in the same fields, immediately adjacent to these trees, were cultivated apples in full bloom, while in Rock Creek Park not more than two miles away the native *M. angustifolia* had not yet begun to show pink in its tiny buds. Near Newark, Delaware, and near Baltimore, Maryland, on May 3, 1942, orchards had passed the height of their bloom and plants of *Malus* "*platycarpa*" were dropping their petals, while nearby plants of *M. coronaria* were still partially in bud. At the foot of Lookout Mountain, in Dade County, Georgia, on April 27, 1941, a "*platycarpa*" tree had dropped most of its petals, as had cultivated trees; native trees in identical situation a few miles down the valley were just coming into flower. Two days later, near Blue Ridge, in Fannin County, Georgia, a specimen of *Malus* "*platycarpa*" was in full bloom along the road, in marked contrast to nearby specimens of *M. angustifolia* that were yet in bud.

Explanation of figure 1.

Fruits of supposed hybrid crabapples, natural size. Three large fruits in upper row are from *McVaugh 5441,* Virginia, neg. 77765; three small round fruits in center are from *McVaugh 5462,* Maryland, neg. 77789; bottom row and the cut fruit are from *McVaugh 5497,* Virginia, neg. 77917. Note variation in size, shape, color values, degree of glaucosity, and length of stem. Negative numbers refer to photographs in the files of the Division of Plant Exploration and Introduction.

In regard to the second of the criteria of hybridity mentioned above, namely the presence of the two supposed parents in the vicinity of the suspected hybrid, it is noteworthy that most if not all the known occurrences of *Malus "platycarpa"* have been in or near inhabited places where both

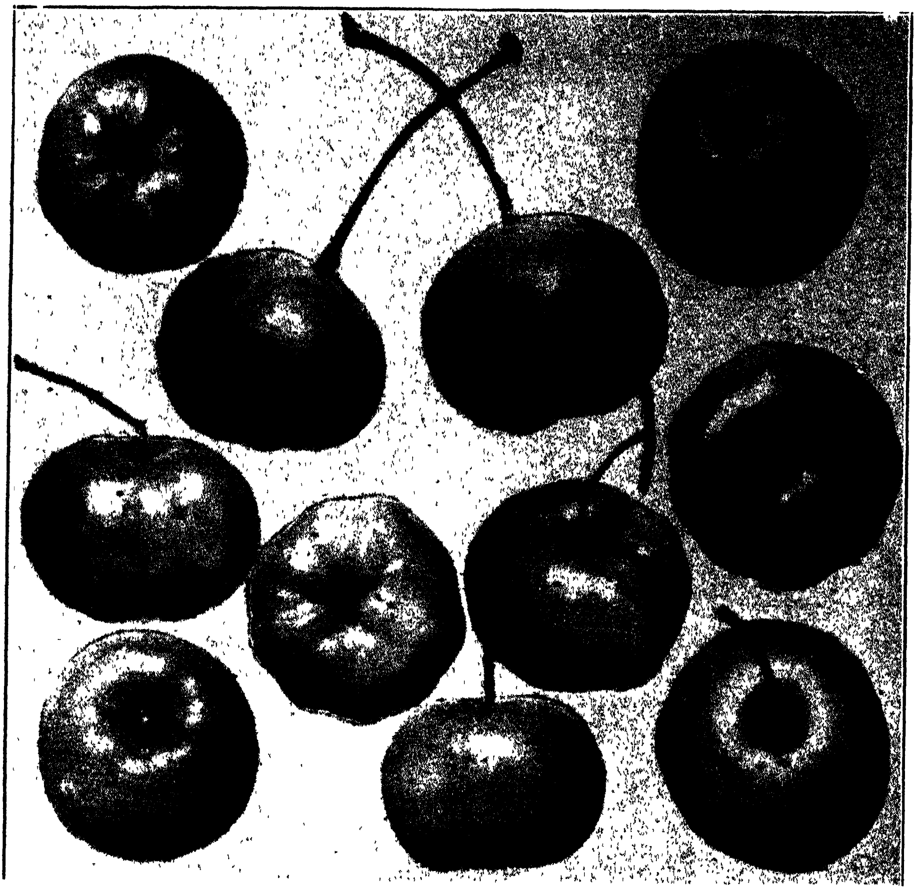


FIG. 2. Fruits of native American crabapples, natural size. Top row, *Malus angustifolia* (Ait.) Michx., from a collection by O. M. Freeman, District of Columbia. The fruit is often lopsided (second from left) and the thickened peduncle is characteristic. Neg. 77763. Second row, *Malus glabrata* Rehd., from *McVaugh 5495*, a cultivated tree at Ithaca, New York. The fruit is yellow and characteristically flattened and angled; Neg. 77906. Bottom row, *Malus coronaria* (L.) Mill., from *McVaugh 5443*, Perry Co., Pennsylvania; Neg. 77764.

native and cultivated apples were also known. *Malus platycarpa* var. *Hoopesii* (Rehd.) Rehd., one of the many forms of *"platycarpa"* as that group is understood in this paper, originated in a nursery at West Chester,

Pennsylvania, and was sent to the Arnold Arboretum in 1876. According to notes made by T. G. Harbison, who collected the original specimens of *Malus platycarpa,* the species occurred as "scattered trees . . . near Franklin [North Carolina] at a distance of from 3 to 15 miles from the [original] locality." Harbison is also quoted as saying "As this tree grows in the fertile soil of bottoms it has been nearly exterminated by the clearing of the valleys."

In 1929, Doctor S. F. Blake discovered a thicket of "*platycarpa*" crabapples in Arlington, Virginia, on the outskirts of Washington, and more recently additional trees have been found a few miles further south, near the Arlington-Alexandria boundary. A thicket comprising thousands of plants of vigorously growing crabapples borders the main highway to Philadelphia at the eastern boundary of the City of Baltimore, where these trees seem to compete favorably with ordinary wild plants in the vicinity. Further northeast, just south of Newark, Delaware, in a long-settled and intensively farmed area, several large trees of "*platycarpa*" occur in a pasture. Further south and west suspected hybrids occur along roadsides near McArthur, Ohio, near Hendersonville, North Carolina, and at several places in northern Georgia.

It is not always possible, naturally, to find cultivated apples, native crabs, and the putative hybrids between them, all growing happily together in the same thicket. In all the localities enumerated above, however, both possible parent types are known to occur, either in the immediate vicinity of the supposed hybrids, or, at most, at distances of a few miles. Cross-pollination by insects is often effected over distances of this order of magnitude, and birds, or other animals, frequently carry seeds or whole fruits to similar distances from the parent plants, so that in this one respect a hybrid origin for all the known plants of *Malus "platycarpa"* is entirely possible.

The third criterion of hybridity, again to quote Professor Bailey, is "occurrence usually in small numbers, as if incidental or exceptional to the main population." Without exception the plants of *Malus "platycarpa"* known to me are isolated or anomalous trees, local in occurrence and differing markedly from the remainder of the apple population in the vicinity. There are apparent exceptions to this near Baltimore and near Washington where *Malus "platycarpa"* reproduces exceptionally well by seed, forming extensive thickets. A clue to this behavior is found, however, in the fact that the seedlings making up these thickets agree with their elders exactly, leaf for leaf and feature for feature. Other species of *Malus,* and species of related genera, including *Crataegus,* are known to behave in exactly this fashion; triploid and other types, apparently of hybrid origin, come true from seed even when exposed to foreign pollen. Some of these do not develop viable pollen of their own and are thought to have developed an apogamous or par-

thenogenetic process by which fertile seeds are produced in the absence of any fertilization whatever. Few of the "*platycarpa*" plants have been investigated cytologically,[4] but such an investigation is highly desirable and might settle finally the question of the hybrid origin of these forms. Chromosome counts have been made upon some of the hybrids developed by Professor N. E. Hansen in South Dakota. One of these, Kola, was determined to be a tetraploid ($2n = 68$) by Nebel;[5] other varieties have been investigated by Professor F. B. Lincoln of the University of Maryland, who finds that the chromosome number varies from 34 in some varieties to 51 or 68 in others. The parents of the triploid and tetraploid varieties are themselves said to be normally diploid.[6]

The total of the evidence at hand, although this evidence is chiefly inferential, indicates a probable hybrid origin for a series of forms which have been known collectively as "*Malus platycarpa.*" Although it is clearly unsafe to predicate the hybrid nature of plants known from herbarium specimens alone, it appears from such specimens and from the description of *Malus platycarpa* var. *Hoopesii* and the original *M. platycarpa* of Rehder that these are also to be regarded with suspicion.

Some of the collections referred by botanists to *Malus platycarpa* may have been taken from aberrant individuals of genetically pure species, but it is highly improbable that the entire series of plants discussed in this paper has arisen through variation alone. Much additional information is needed in order satisfactorily to establish the status of these anomalous trees, and botanists and collectors will do well to make ample notes and full collections from them at every opportunity.

Following is a discussion of the material upon which the present paper is based:

DELAWARE: Three miles south of Newark, Newcastle Co., *McVaugh 6494.*[7] Several round-headed open-grown trees in a pasture, the largest about 8 m. tall and with a single trunk about 35 cm. dbh. Branches not at all thorny; leaves slightly lobed on vigorous shoots; pedicels definitely hairy; petals almost all fallen on May 3, 1942; fruit somewhat flattened, not over 4 cm. in diameter, resembling that of native species. Native species are not abundant in this vicinity, but are known to occur locally near Christiana (about 10 miles away) and in southeastern Chester Co., Pennsylvania (at about the same distance).

[4] A report of the occurrence of tetraploidy ($2n = 68$) in *Malus platycarpa* was made recently by F. B. Lincoln and L. P. McCann (Proc. Am. Soc. Hort. Sci. **34**: 26. 1937), but the source of the material was not stated and there appears to be no way to check its authenticity.

[5] Gartenbauwiss. 1: 549–592. 1929.

[6] Proc. Am. Soc. Hort. Sci. 37: 217. 1940; S. Dak. Exp. Sta. Bull. 339: 11. 1940.

[7] Herbarium specimens cited in this paper, unless otherwise indicated, are deposited in the Herbarium of the United States National Arboretum, Washington, D. C.

MARYLAND: Along U. S. Highway No. 40, east of Baltimore City Limits in Baltimore Co., *McVaugh 5462* (Sept. 29, 1940, in fruit) and *5500* (April 20, 1941, in bud). Hundreds of vigorous plants forming extensive thickets over an area more than a mile long; the plants commonly have an upright habit quite distinct from that of the ordinary native apple. Branches not at all thorny; leaves slightly lobed on vigorous shoots; pedicels white-tomentose; petals fallen and fruit slightly enlarged on May 3, 1942; Fruit 3.1–3.7 cm. in diameter, 2.8–3.4 cm. high, greenish-yellow, glaucous, faintly odorous and very slightly waxy; seeds none, or 1–4. Native species are not abundant in this region, but plants occur locally at points 1–5 miles distant. Figures 1, 3.

VIRGINIA: 1. Thickets at corner of Glebe Road and Washington Boulevard, Arlington, *McVaugh 5497* (October 24, 1940, in fruit). From the same thicket, *S. F. Blake 10831* (April 23, 1929, in flower, Oct. 15, 1929, in fruit). About twenty scattered plants on gravelly overgrown hillsides. Branches somewhat thorny; leaves slightly lobed on vigorous shoots; buds beginning to open on April 19, 1942; fruit flattened, 3.9–5.2 cm. in diameter, 2.9–3.5 cm. high, yellowish-green, glaucous, fragrant and slightly waxy; seeds usually about 5. Native crabapples are scarce in this region; a few supposedly native plants of *Malus angustifolia* are known from the District of Columbia. Figures 1, 3.

2. Abandoned pasture, lowlands called "Hell's Bottom," south of Columbia Pike and east of Arlington Ridge Road, Arlington, *McVaugh 5141, 5442* (September 15, 1940, in fruit). Specimens from the same locality, *F. R. Fosberg 16971* (flower) and *17432* (fruit), are to be distributed. About twenty small trees associated with cultivated apple (seedlings?). Branches not or but slightly thorny; leaves lobed on shoots, suggesting the shoot-leaves of *Malus angustifolia* (fig. 3); pedicels hairy; buds "ballooned" on April 19, 1942; fruit flattened, 3.5–4.5 cm. in diameter, 2.5–3.5 cm. high, greenish-yellow, usually with a red cheek, glaucous, almost without fragrance and waxy covering (fig. 1); seeds 4–10.

NORTH CAROLINA: 1. Roadside thickets 4.5 miles north of Hendersonville, Henderson Co., *McVaugh 5632*. A single tree about 6 m. tall, with spiny branches, associated with *Malus angustifolia* and cultivated apples. Leaves not lobed; plant in full bloom on April 30, 1941, when *M. angustifolia* in the same thicket was still partially in bud; pedicels hairy or tomentose; anthers yellow or very faintly pinkish; fruit unknown. Native crabapples are abundant in this region.

2. Roadside 3.4 miles west of Franklin, Macon County, *McVaugh 5624*. A single plant; branches not spiny; growth and bark like those of the cultivated apple; leaves very slightly lobed on vigorous shoots; plant in full bloom on April 29, 1941, slightly in advance of nearby trees of *M. angustifolia;* pedicels hairy; anthers cream-yellow, slightly pink-tinged; fruit unknown. Native crabapples are abundant in this region.

3. Edge of cultivated field 4.2 miles northwest of Andrews, Cherokee Co., *McVaugh 5618*. A single open-grown tree about 6 m. tall, the branches scarcely spiny; leaves somewhat lobed on vigorous shoots; pedicels hairy; flowers almost all open on April 29, 1941, somewhat in advance of nearby native trees; fruit of the last (1940) season fallen at this date, mostly about 4 cm. in diameter, a little longer than broad, slightly sheep-nosed. Native apples are not abundant in this region, but occur sparingly throughout.

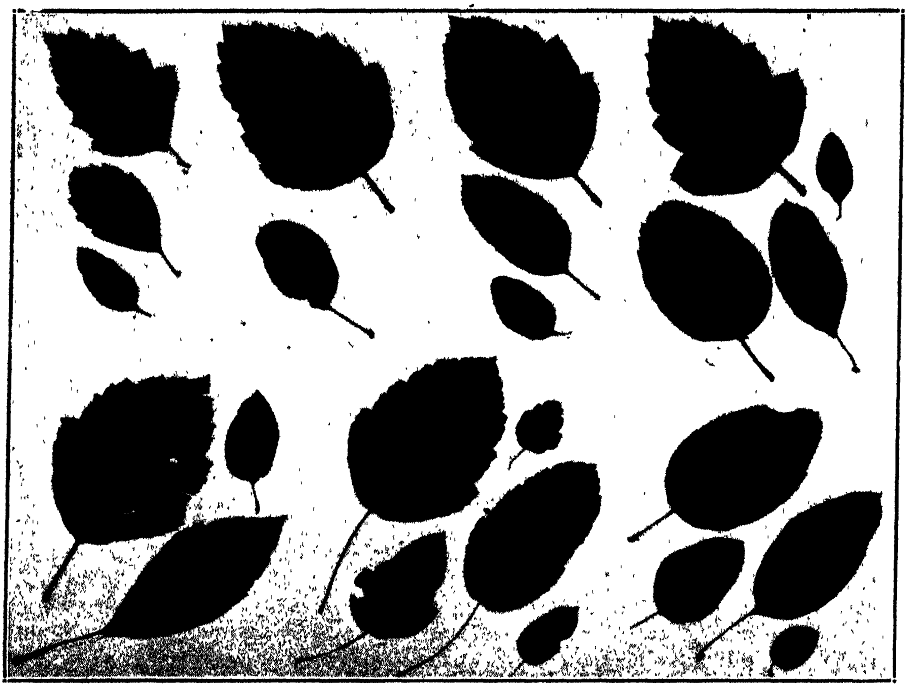


FIG. 3. Leaves of representative American crabapples and supposed hybrids, in seven groups. Each group comprises two or more leaves from a single tree, including the following types; 1) A large leaf from a vigorous shoot; this leaf indicates the maximum size and maximum degree of lobing for the tree in question. 2) Leaves from the base of vigorous shoots or those produced by fruit-spurs after the flowering season; these two types are indistinguishable. Leaves of this sort are regularly smaller and narrower than the lobed leaves from vigorous shoots. 3) Small leaves from the fruit-spurs; these are present at flowering time and persist until late in the season; they are usually not lobed except in *M. glabrata* and in forms of *M. coronaria* and *M. ioensis*. Neg. 79705. All leaves about ⅝ natural size.

Bottom row, left to right:

M. "platycarpa," McVaugh 5462, Baltimore, Maryland. Note the relatively long petioles in this group and two following.

M. coronaria (L.) Mill., *B. Long 16985* (in herb. Morris Arboretum), from Newcastle Co., Delaware (three largest leaves), and *McVaugh 6495,* Chester Co., Pennsylvania (two small leaves). Note that lobed and unlobed leaves may be found on the same plant. Some forms of *M. coronaria* have more strongly lobed leaves, with sharper serrations, than do those shown here.

M. "platycarpa," McVaugh 5765, Vinton Co., Ohio.

Top row, left to right:

M. angustifolia, McVaugh 5227, Talbot Co., Georgia. This is not an unusual leaf-form in this species, although forms with crenate leaves are common. Note the short petioles in this group and the three following.

M. platycarpa Rehd., *Harbison,* "April 22, 1911," from Macon Co., North Carolina (in U. S. National Herbarium). The date is apparently erroneously given; the maturity of the specimen indicates that it was collected in the fall.

M. "platycarpa," McVaugh 5497 (two at top) and *Blake 10831* (at bottom), Arlington, Virginia.

M. "platycarpa," McVaugh 5441, Arlington, Virginia.

GEORGIA: 1. Roadside, edge of field, 2.2 miles east of Blue Ridge Hotel, Blue Ridge, Fannin Co., *McVaugh 5614*. A single open-grown tree about 6 m. tall; branches not spiny; growth and bark like those of the cultivated apple; leaves not lobed; pedicels and calyx hairy; plant in full bloom on April 29, 1941, slightly in advance of trees of *M. angustifolia* in the same valley about 2 miles further west; fruit unknown.

2. Pasture on Bible Farm 1 mile north of Sulphur Spring Station, Dade Co., *McVaugh 5594*. A single open-grown tree about 8 m. high. Branches not spiny; leaves not lobed; pedicels and calyx more or less tomentose; petals almost all fallen on April 27, 1941; on the same day *Malus angustifolia* at Valley Head, Alabama (also at the foot of Lookout Mountain) was in full bloom, and at the summit of Lookout Mountain near DeSoto Falls the same species was in bud. Native crabapples are abundant in this region.

OHIO: Roadside bank in woods above stream, 4 miles northwest of McArthur, Vinton Co., *McVaugh 5765*, July 4, 1941. A single tree about 5 m. tall; branches scarcely spiny; leaves and habit like those of the cultivated apple, the leaves not at all lobed except on the most vigorous shoots; pedicels hairy at the above date; flowers and mature fruit unknown; core of immature fruit that of the section Chloromeles. Figure 3. Native crabapples occur throughout this region.

SUMMARY

At various localities in eastern United States occur trees which are certainly derived from native American sources but which do not comprise a homogeneous stock and which 1) Occur as anomalous or isolated individuals or groups in the midst of undoubted native populations, and 2) are morphologically and physiologically intermediate between native species and the introduced, cultivated apple. This series of forms is usually characterized by fruit larger than that of the American crabapples and by leaves possessing a lesser degree of lobing than those of the native species. Most of these forms have been called "*Malus platycarpa* Rehd." or "*Malus platycarpa* var. *Hoopesii* (Rehd.) Rehd." It is inferred from observation and from comparison with hybrids of known parentage that most, if not all, of the plants previously referred to *Malus platycarpa*, including probably the original material and that of var. *Hoopesii*, are of hybrid origin. It is supposed that hybridization has taken place between cultivated apples and native species of *Malus*, section *Chloromeles*, occurring in the same region. Experimental proof is needed to confirm this hypothesis.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,
BUREAU OF PLANT INDUSTRY,
U. S. DEPARTMENT OF AGRICULTURE, BELTSVILLE, MD.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 4, pp. 430–435 JULY, 1943

CHROMOSOMES OF ASTRAGALUS

HILDA VILKOMERSON

Some species of *Astragalus* absorb and accumulate selenium from seleniferous soils; other, closely related species do not (15). Preliminary to a genetic study of this physiological variation, a survey was made of the chromosome number relationships in 26 North American species of *Astragalus*, whose responses to selenium have been determined by Beath and by Trelease (1, 15).

Germinating seeds of the various species were obtained from Prof. Sam F. Trelease. Chromosome numbers were counted from metaphase plates of seedling root-tips fixed in Craf (modified Navashin) fluid, sectioned at 12 μ (Randolph's card technique (8) being used for handling large numbers of roots), and stained with Newton's crystal violet–iodine.

Of the 26 species studied, 11 have 24 chromosomes (2n; fig. 1). All these are selenium absorbers, as is also the one 44-chromosome species (fig. 2). One species, a non-absorber, has 16 chromosomes (fig. 3). Thirteen species have 22 chromosomes (fig. 4), and of these, four are selenium absorbers, nine non-absorbers.[1] From Table 1 it is evident that members of the *Lonchocarpi* or of the *Podo-sclerocarpi* groups are the desirable species for genetic study of selenium absorption, since these groups include species of like chromosome number and unlike reaction to selenium.

With a single exception, the karyological evidence supports the taxonomic grouping of M. E. Jones' revision of the genus (4). His group *Galegiformes*, however, includes species which differ both in selenium response and in chromosome number (*Astragalus Drummondii* and *A. racemosus*). According to Rydberg's classification (12), too, these species would be grouped together in the genus *Tium* (table 2). Likewise, the cytological findings do not support the unity of Rydberg's genus *Cnemidophacos*. Physiologically this group of species is homogeneous; but here the disparity in chromosome number is paralleled by considerable morphological divergence (4). Indeed, Rydberg in earlier treatments of this material (9, 10) had recognized this difference by using two generic names—*Cnemidophacos* for *A. flavus* and *A. confertiflorus*, and *Ctenophyllum* for *A. Grayi* and *A. pectinatus*. Gray made a like distinction (3). As for Rydberg's *Phaca Preussii*, his earlier grouping of

[1] One species of the very closely related genus *Oxytropis*—*O. pinetorum* (Heller) Rydb. (*O. saximontana* Nels.), which is an important "loco" weed, though not a selenium absorber—was studied. The 2n number is 48. Some so-called loco weeds actually belong in the genus *Astragalus* (e.g., *A. mollissimus* and *A. Earlei*); seedlings of these, however, were not available for study.

this species with *Jonesiella Pattersoni* and *J. praelongus* (11) would seem justified.

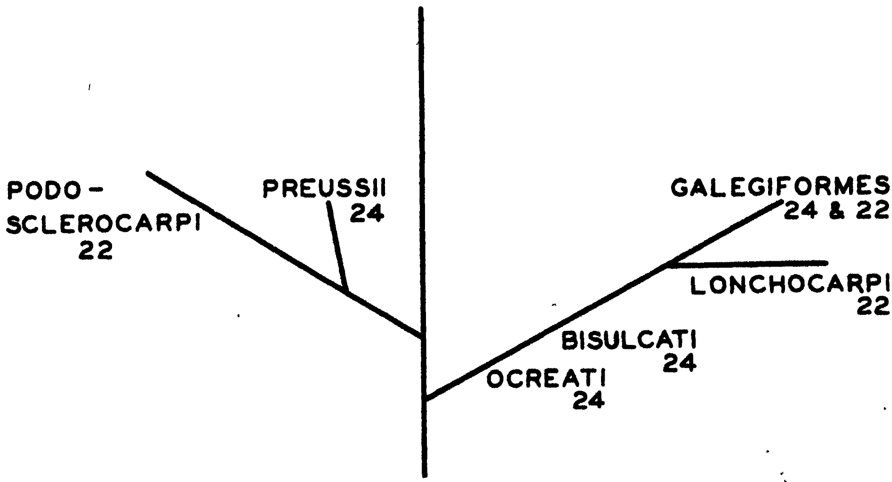
In previous cytological studies of *Astragalus*, ten workers (14) have reported chromosome numbers for 44 Old World species and 4 New World

TABLE 1

Species (Jones' revision)	Selenium absorption	Chromosome number (2n)
Inflati		
Astragalus lentiginosus var. *palans* Jones	–	22
Podo-sclerocarpi		
A. toanus Jones	+	22
A. rafaelensis Jones	+	22
A. Grayi Parry	+	44
A. pectinatus Dougl.	+	22
A. Casei Gray	–	22
A. pterocarpus Wats.	–	22
A. tetrapterus Gray	–	22
A. sclerocarpus Gray	–	22
A. cañonis Jones	–	22
Preussii		
A. Preussii Gray	+	24
A. limatus Sheld.	+	24
A. Pattersonii Gray	+	24
A. praelongus Sheld. (*Pattersonii* var.)	+	24
A. Beathii Porter	+	24
Uliginosi		
A. canadensis Tourn. in L. (= *A. carolinianus* MacMill., not L.)	–	16
Sarcocarpi		
A. crassicarpus Nutt.	–	22
Ocreati		
A. confertiflorus Gray	+	24
A. flavus Nutt. (*confertiflorus* var. *flaviflorus* Kuntze)	+	24
Bisulcati		
A. haydenianus Gray	+	24
A. bisulcatus (Hook.) Gray	+	24
A. oocalycis Jones	+	24
Galegiformes		
A. racemosus Pursh	+	24
A. Drummondii Hook	–	22
Lonchocarpi		
A. Osterhoutii Jones	+	22
A. lonchocarpus Torr.	–	22

species. Thirty-three of these have the 2n number 16, three species have 32, one 36, four 48, five 64, and one 96. There is one 28-chromosome species. Both Senn (13) and Kreuter (6, 7) emphasize the consistency of the basic chromosome number 8 throughout the Galegeae, and the latter cites *Astragalus* as an "especially beautiful example" of this uniformity. Even though

only a small percentage of the species of this enormous genus has been studied (it contains some 1500 species), this strict uniformity is not wholly borne out by the data on our North American species. To fit the pattern of the species previously studied (basic numbers 7 and 8), we might derive the 24- and 22-chromosome groups from hybrids of species with 32 and 16 chromosomes and 28 and 16 chromosomes, respectively. Such triploid species would be highly unstable, however, owing to irregular meiotic pairing. The 22-chromosome group could have arisen by aneuploid loss from a 24-chromosome form. Indeed Kreuter (7) indicated the possibility that further study might be expected to show *Astragalus* species which had "arisen by a diminution" of chromosome number. Somewhat suggestive of such a relationship is this portion of the phylogenetic tree proposed for *Astragalus* in Jones' monograph. (The selenium-absorbing species, apparently, are restricted to these two branches.)



But in the Leguminosae, as in the Cruciferae, aneuploidy is a common relation between tribes and between genera, but not within genera (13). There remains, then, only the assumption of the basic numbers 8, 11, and 12 for our species.

The sporadic occurrence of isolated polysomatic cells is not uncommon in *Astragalus,* nor is it restricted to this genus of the Leguminosae. Tschechow

TABLE 2

Species (Rydberg's revision)	Selenium absorption	Chromosome number (2n)
Homalobus podocarpus (Hook.) Rydb. (*A. sclerocarpus*)	–	22
Diholcos bisulcatus (Hook.) Rydb.	+	24
D. haydenianus (Gray) Rydb.	+	24
D. oocalycis (Jones) Rydb.	+	24

TABLE 2 (*Continued*)

Species (Rydberg's revision)	Selenium absorption	Chromosome number (2n)
Cnemidophacos flavus (Nutt.) Rydb.	+	24
C. confertiflorus (Gray) Rydb.	+	24
C. toanus (Jones) Rydb.	+	22
C. rafaelensis (Jones) Rydb.	+	22
C. Grayi (Parry) Rydb.	+	44
C. pectinatus (Dougl.) Rydb.	+	22
Xylophacos Casei (Gray) Rydb.	–	22
Pterophacos pterocarpus (Wats.) Rydb.	–	22
P. tetrapterus (Gray) Rydb.	–	22
Lonchophaca macrocarpa (Gray) Rydb. (*A. lonchocarpus*)	–	22
L. Osterhoutii (Jones) Rydb.	+	22
Phaca Preussii (Gray) Rydb.	+	24
P. Crotalariae Benth. (*A. limatus*)	+	24
Tium Drummondii (Dougl.) Rydb.	–	22
T. racemosum (Pursh) Rydb.	+	24
T. palans (Jones) Rydb.	–	22
Brachyphragma Serenoi (Kuntze) Rydb. (*A. cañonis*)	–	22
Jonesiella Pattersoni (Gray) Rydb.	+	24
J. praelonga (Sheld.) Rydb.	+	24
Astragalus canadensis L.	–	16
Geoprumnon crassicarpum (Nutt.) Rydb.	–	22

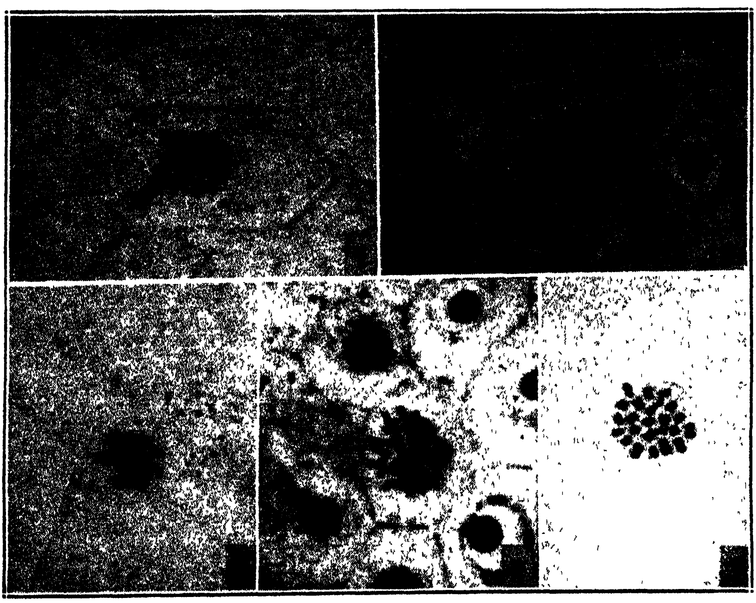


FIG. 1. Somatic metaphase of *Astragalus Preussii* (2n = 24). FIG. 2. *A. Grayi* (2n = 44). FIG. 3. *A. canadensis* (*carolinianus*) (2n = 16). FIG. 4. *A. toanus* (2n = 22). FIG. 5. Polysomaty in *A. cañonis*, showing 22 pairs of chromosomes. In later divisions, such cells show 44 chromosomes, unpaired.

(16, 17) reported such cells in two of the species he studied—*A. altaicus* and *A. candidissimus*. In the latter, indeed, he sometimes found tetraploid numbers (syndiploid he calls them) in up to 40 per cent of the metaphase plates. In our material such cells were found in three of the species studied—*A. Drummondii*, *A. toanus*, and *A. cañonis*—but here they were very rare (fig. 5). Polysomatic cells have been reported, in varying degrees of frequency, for species of several other leguminous genera: *Acacia*, *Albizzia*, *Canavalia*, *Cassia*, *Cicer*, *Glycine*, and *Phaseolus* (2, 5, 6, 17).

SUMMARY

Chromosome numbers are reported for 26 North American species of *Astragalus* and are correlated with selenium absorption data. Possible phylogenetic interrelations are discussed. Polysomaty is reported in three species.

The author is grateful to Professors M. M. Rhoades and Sam F. Trelease for their interest and helpful suggestions.

DEPARTMENT OF BOTANY, COLUMBIA UNIVERSITY
NEW YORK

Literature Cited

1. **Beath, O. A., Gilbert, C. S. & Eppson, H. F.** The use of indicator plants in locating seleniferous areas in western United States. IV. Progress report. Am. Jour. Bot. **28**: 887–900. 1941.
2. **Ghimpu, V.** Sur l'existence simultanée des mitoses diploïdes, didiploïdes, et tetradiploïdes chez les *Acacia*. Compt. Rend. Soc. Biol. **101**: 1122–1123. 1929.
3. **Gray, Asa.** A revision . . . of the North American species of *Astragalus* and *Oxytropis*. Proc. Am. Acad. **6**: 188–236. 1864.
4. **Jones, Marcus E.** Revision of North American species of *Astragalus*. 1923.
5. **Karpechenko, G. D.** On the chromosomes of Phaseolinae. Bull. Appl. Bot. Pl. Breed. **14**[2]: 143–148. 1925.
6. **Kreuter, Erich.** Chromosomenstudien bei den Galegeen. Ber. Deuts. Bot. Ges. **47**: 99–101. 1929.
7. ———. Beitrag zu karyologisch-systematischen Studien an *Galegeen*. Planta **11**: 1–44. 1930.
8. **Randolph, L. F.** Card mounts for handling root tips in the paraffin method. Stain Techn. **15**: 45–48. 1940.
9. **Rydberg, Per Axel.** *Astragalus* and its segregates as represented in Colorado. Bull. Torrey Club **32**: 657–668. 1905.
10. ———. Studies on the Rocky Mountain flora—28. Bull. Torrey Club **40**: 43–74. 1913.
11. ———. Flora of the Rocky Mountains. 1917.
12. ———. Fabaceae: Galegeae. N. Am. Flora **24**: 251–462. 1929.
13. **Senn, Harold A.** Chromosome number relationships in the Leguminosae. Bibl. Genet. **12**: 175–345. 1938.
14. **Tischler, G.** Pflanzliche Chromosomen-zahlen. IV. Tabulae Biologicae **16**: 162–218. 1938.

15. **Trelease, Sam F.** Identification of selenium indicator species of *Astragalus* by germination tests. Science **95**: 656–657. 1942.

16. **Tschechow, W.** Karyologisch-systematische Untersuchung des Tribus Galegeae, Fam. Leguminosae. Planta **9**: 673–680. 1930.

17. **Tschechow, W. & Kartaschowa, N.** Karyologisch-systematische Untersuchung der Tribus Loteae und Phaseoleae. Unterfam. Papilionatae. Cytologia **3**: 221–249. 1932.

VOL. 70, No. 4, pp. 436–439 JULY, 1943

INJURIES TO TREES CAUSED BY CELASTRUS AND VITIS[1]

H. J. LUTZ

Observations by the writer over a period of years have revealed that bittersweet (*Celastrus scandens* L.) and grape (*Vitis aestivalis* Michx., *V. vulpina* L., *V. labrusca* L., and *V. bicolor* Le Conte) vines cause distinctive injuries to the stems and branches of young trees. These climbers, which are common or locally abundant in the forests of the eastern United States, are relatively intolerant of shade and are encountered most frequently in stands of young trees, in understocked stands and near forest borders. In other words, they are most abundant in stands representing early stages of successional development; as stand density increases the number and vigor of the vines decreases. South and west slopes appear more favorable for their development than are north and east slopes. Other vines such as poison ivy (*Rhus toxicodendron* L.) and the Virginia creeper (*Psedera quinquefolia* (L.) Greene) climb trees but they do not twine around the stems so as to cause constrictions. Poison ivy climbs by means of rootlets whereas the Virginia creeper has tendrils which are usually terminated by enlarged adhesive discs.

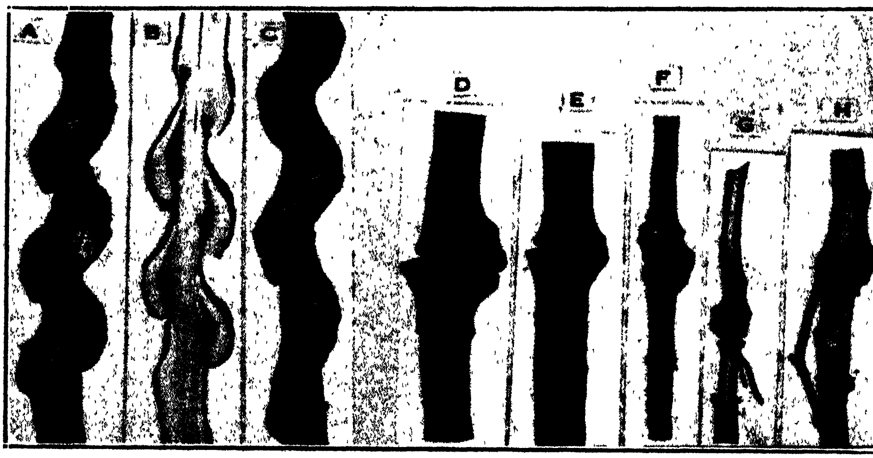


FIG. 1. A, B, and C, stems of *Sassafras albidum* (Nutt.) Nees. showing the injury caused by *Celastrus scandens* L. B, a longitudinal section through the stem A (1/10 natural size). D to H, stems injured by *Vitis* spp. D, E, and F, *Acer rubrum* L. G, *Acer saccharum* Marsh. H, *Hamamelis virginiana* L. (½ natural size).

[1] Illustrations published with the aid of the Lucien M. Underwood Memorial Fund.

The injury resulting from bittersweet is caused by the vines twining tightly around stems and branches of young trees and inhibiting, if not completely stopping, downward translocation of organic solutes. These organic substances, which are elaborated in the leaves, move downward through the tree stem in what is sometimes referred to as the "descending stream of assimilates." The pathway of this descending stream is very largely through the phloem, or more specifically, through the sieve tubes in the phloem. When normal movement of organic materials is prevented by constriction of

FIG. 2. Stems of *Liriodendron tulipifera* L. (left) and *Pinus strobus* L. (right) injured by bittersweet (1/10 natural size). The longitudinal sections show the character of the internal injury.

the phloem these substances accumulate in the region immediately above the point where stoppage occurred. The situation is quite analogous to that which exists when a tree stem or branch is subjected to ringing, that is, when the tissues external to the xylem are completely removed.

In twining around a tree stem the bittersweet vine takes a spiral course, the angle formed with the horizontal usually being between 50 and 70 degrees. With this relatively low pitch of the spiral, friction between the tree stem and vine stem is sufficiently great to prevent the latter from being

loosened to accommodate radial growth of the tree. Consequently, normal radial growth of the tree stem continues for only a brief period, usually one or two years, after the vine has become attached. Bittersweet is a dextrorse climber.

As a result of the damming of the descending stream, increment immediately above a constricting vine is greatly increased whereas immediately below increment is greatly lessened, or may cease. This is illustrated in figures 1 (A, B, C) and 2.[2] Trees usually are not killed by bittersweet vines because new conductive tissues are formed in which the axes of the elements are parallel to the spiral constrictions. Figure 3 illustrates this change in

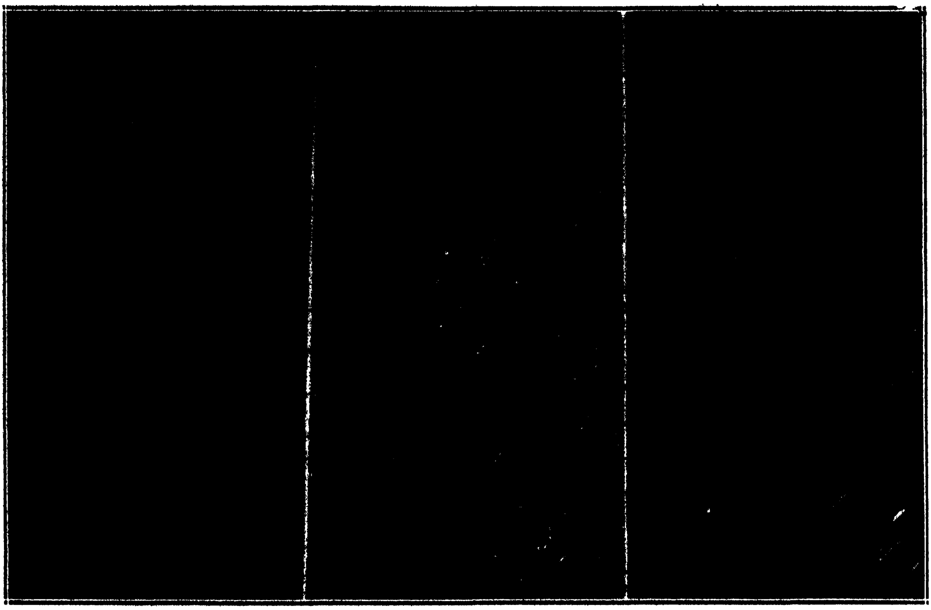


FIG. 3. Serial tangential sections showing the orientation of elements in a sassafras stem injured by bittersweet. In the section at the left, from a plane near the center of the stem, the orientation is normal. These tissues were developed before the injury. The section in the center, from a plane midway between the pith and the outside, shows the elements oriented approximately parallel to the spiral constriction. The section at the right shows an even more extreme change in orientation of elements in the outermost growth layers (× 50).

orientation of elements in a sassafras stem. In stems such as those shown in figure 1 (A, B, C) the course taken by the downward moving organic solutes is a spiral.

[2] An injury similar to that caused by bittersweet is figured as the frontispiece in the April, 1942, issue of the Journal Forestière Suisse. The illustration referred to shows the effect of a honeysuckle vine on a young ash stem. It is obvious that the longitudinal section figured in the Swiss journal is upside down.

Not infrequently death of young trees has resulted from the presence of vines. With the flow of organic solutes to the roots stopped, the reserve food materials are gradually used up and the parts below the constriction die of starvation. In these cases the development of new conductive tissue was evidently so slow that the roots died before their organic food supply could be reestablished. As long as the roots remain alive upward conduction of water and inorganic solutes takes place even though the constricting vines may prevent the downward movement of organic assimilates. This is explained by the fact that the pathway of the upward moving stream is through the xylem.

Trees have been encountered which, though girdled, continued to live, in spite of the fact that downward movement of organic substances to the roots seemed impossible. It is likely that the roots of these injured trees were obtaining their organic nutrients from adjacent normal trees to which they were root-grafted. Root-grafting is evidently very common in forest trees.

In addition to the damage resulting from occlusion of bittersweet vines and bark in tree stems and the development of very abnormal wood structure, avenues are opened for entry of decay and wood borers which may render the affected trees worthless. All species of trees are subject to injury but hardwoods are more commonly damaged than conifers. The relatively dense crowns of the latter result in unfavorable light conditions for the intolerant bittersweet.

Grape vines cause a minor but interesting type of injury as a result of their tendrils coiling tightly around small tree stems and branches. Injuries of this character are illustrated in figure 1 (D to H). The tendrils cause a deformation of the tree parts analogous to that resulting from bittersweet and very frequently are occluded in the stems or branches. It is not uncommon to find a stem or branch so weakened by a tendril that it has broken off at the point of constriction.

The most serious injury from grape vines, and from other climbers such as poison ivy and the Virginia creeper, is the deformation and shading of tree crowns which they cause. Substantial damage to seedlings and middle-aged trees is commonly seen. During cultural operations in the forest it is good practice to sever the stems of all vines which are climbing trees. Exceptions may be made where the owner wishes to retain the vines as sources of food for wild life.

School of Forestry, Yale University
New Haven, Connecticut

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)

(See also under Morphology: **Camp & Gilly**; under Genetics: **Anderson & Hubricht, Smith**)

Abbiatti, D. Sinopsis de las Lorantáceas argentinas. Rev. Arg. Agron. **10**: 1–25. *f. 1–6.* Mr 1943.

Acosta Solis, M. Estudio botanico farmocognósico de la Achicoria de Quito. Flora **2**: 79–97. *f. 1–27.* D 1942.

Adams, J. W. A double-flowered form of *Gillenia trifoliata.* Rhodora **45**: 215, 216. My 1943.

Allard, H. A. The probable relationship of *Phaseolus polystachios* to other species. Rhodora **45**: 169, 170. My 1943.

Allard, H. A. & Leonard, E. C. The vegetation and floristics of Bull Run Mountain, Virginia. Castanea **8**: 1–64. *f. 1–7.* Ja–Mr [13 My] 1943.

Ames, O. & Correll, D. S. A new *Cattleya* from Guatemala. Am. Orchid Soc. Bull. **11**: 400–402. *pl. 11.* 9 Ap 1943.

Anderson, J. P. Papers on the flora of Alaska—I. The Genus *Cicuta.* Torreya **42**: 176–178. *f. a–d.* N–D 1942 [24 Ap 1943].

Asplund, E. Una nueva especie de *Isöetes* en el Ecuador. Flora **2**: 73–77. *1 f.* D 1942.

Bailey, I. W., Nast, C. G. & Smith, A. C. The family Himantandraceae. Jour. Arnold Arbor. **24**: 190–206. *pl. 1–6.* Ap 1943.

Bettle, A. A. A key to the North American species of the genus *Scirpus* based on achene characters. Am. Midl. Nat. **29**: 533–538. *pl. 1, 2.* Mr [Ap] 1943.

Benner, W. M. Additions to the flora of Bucks County, Pennsylvania—III. Bartonia 22: 3, 4. 7 My 1943.

Benson, L. Revisions of status of southwestern desert trees and shrubs. Am. Jour. Bot. **30**: 230–240. Ap 1943.

Bergner, A. D. [& Blakeslee, A. F.] Geographical distribution of chromosomal types in *Datura metel.* Am. Jour. Bot. **30**: 222–230. *f. 1–6.* Ap 1943.

Braun, E. L. An annotated catalog of Spermatophytes of Kentucky. 1–161. *f. 1–6.* Cincinnati, Ohio, S. Swift, 1943.

Brown, R. W. A climbing fern from the Upper Cretaceous of Wyoming. Jour. Wash. Acad. **33**: 141, 142. *f. 1–5.* 15 My 1943.

Cain, S. A. The tertiary character of the cove hardwood forests of the Great Smoky National Park. Bull. Torrey Club **70**: 213–235. 1 My 1943.

Camp, W. H. & Gilly, C. L. The structure and origin of species. Brittonia **4**: 323–385. Mr. [10 Ap] 1943.

Carabia, J. P. Plantae cubensis novae I. Mem. Soc. Cubana Hist. Nat. **17**: 15–18. 3 Ap 1943.

Clausen, R. T. *Carex aestivalis* and *Carex lurida* var. *gracilis* on the glaciated Allegheny Plateau. Torreya **42**: 174–176. N–D 1942 [24 Ap 1943].

Clausen, R. T. The section *Sedastrum* of *Sedum*. Bull. Torrey Club **70**: 289–296. *f. 1*. 1 My 1943.

Clausen, R. T. Studies in the Ophioglossaceae: *Botrychium*, subgenus *Sceptridium*. Am. Fern Jour. **33**: 11–27. Ja–Mr [1 Ap] 1943.

Clausen, R. T. A new name for Rose's *Sedum nutans*. Cactus & Succ. Jour. **15**: 63, 64. *f. 31*. My 1943.

Constance, L. A new species of *Phacelia* from Saline Valley, California. Madroño **7**: 56–59. *pl. 3*. Ap 1943.

Cory, V. L. The *Senecio* on the coastal dunes of Texas. Rhodora **45**: 164–166. 10 Ap 1943.

Craig, R. T. *Mammillaria Woodsii* sp. nov. Cactus & Succ. Jour. **15**: 33, 34. *f. 18, 19*. Mr 1943.

Croizat, L. A new variety of *Euphorbia pteroneura* Berger (*E. Floresii* Standl.) Desert **15**: 21–23. F [Ap] 1943.

Croizat, L. Novelties in American Euphorbiaceae. Jour. Arnold Arb. **24**: 165–189. Ap 1943.

Croizat, L. What is the trinomial *typicus?*—I. Bull. Torrey Club **70**: 310–324. 1 My 1943.

Cronquist, A. The North American species of *Erigeron* centering about *E. speciosus* (Lindl.) DC. and *E. glabellus* Nutt. Bull. Torrey Club **70**: 265–274. 1 My 1943.

Cronquist, A. Revision of the western North American species of *Aster* centering about *Aster foliaceus* Lindl. Am. Midl. Nat. **29**: 429–468. *pl. 1–17*. Mr [Ap] 1943.

Dayton, W. A. The names of the giant *Sequoia*. Leafl. West. Bot. **3**: 209–219. 30 Ap 1943.

Diddell, M. W. *Polypodium pectinatum* as an epiphyte. Am. Fern Jour. **33**: 29. Ja–Mr [1 Ap] 1943.

Diddell, M. W. & Shields, E. M. A moss new to Florida. Bryologist **46**: 22, 23. Mr [10 My] 1943.

Dole, W. H. Hart's-tongues in a limestone grotto. Am. Fern Jour. **33**: 30. Ja–Mr [1 Ap] 1943.

Dixon, H. N. War zone mosses. Bryologist **46**: 14–22. Mr [12 My] 1943.

Dunkle, M. B. Contributions from the Los Angeles Museum—Channel Islands Biological Survey. 28. Three new plants from San Clemente Island. Bull. S. Cal. Acad. **42**: 31–33. 15 My 1943.

Eames, A. J. & St. John, H. The botanical identification of the Hawaiian Ipu Nui or large gourd. Am. Jour. Bot. **30**: 255–259. *f. 1–3*. Ap 1943.

Eastwood, A. Some veronicas in Golden Gate Park. Leafl. West. Bot. **3**: 220–222. 30 Ap 1943.

Epling, C. The American species of *Scutellaria*. Cal. Pub. Bot. **20**: 1–146. *pl. 1–3 + 1–10*. 21 Jl 1942.

Ewan, J. *Asplenium septentrionale* in California. Am. Fern Jour. **33**: 29. Ja–Mr [1 Ap] 1943.

Ewan, J. The correct name for the Pacific involucrate *Trifolium*. Leafl. West. Bot. **3**: 222–224. 30 Ap 1943.

Eyles, M. S. & Eyles, D. E. A local flora of the Reelfoot Lake region of West Tennessee. Jour. Tenn. Acad. **18**: 108–136. Ja [3 Ap] 1943.

Farwell, O. A. Fern notes, IV: Supplementary remarks on the ferns of the Keweenaw Peninsula, Michigan. Am. Fern Jour. **33**: 8–10. Ja–Mr [1 Ap] 1943.

Fassett, N. C. Some new forms from the Middle West. Torreya **42**: 179–181. *illust.* N–D 1942 [24 Ap 1943].

Fernald, M. L. The fruit of *Dirca palustris.* Rhodora **45**: 117–119. 10 Ap 1943.

Fernald, M. L. *Scirpus Peckii* in Canada. Rhodora **45**: 168. 10 Ap 1943.

Gilly, C. L. A preliminary investigation of the North American canes (*Arundinaria*). Bull. Torrey Club **70**: 297–309. *f. 1, 2.* 1 My 1943.

Goodman, G. J. Notes on *Chorizanthe.* Leafl. West. Bot. **3**: 230. 30 Ap 1943.

Goodwin, R. H. The flora of Mendon Ponds Park. Proc. Rochester Acad. **8**: 233–298. *f. 1–6.* 27 Ap 1943.

Gordon, R. B. The "Darlington Herbarium" at West Chester. Bartonia 22: 6–9. 7 My 1943.

Graham, E. & McMinn, H. E. Ornamental shrubs and woody vines of the Pacific Coast, with a chapter on the structure and functions of flowering plant organs. 1–259. *pl. 1–22 + f. 1–44.* Berkeley, Cal., Gillick Press, 1941.

Grant, E. & Epling, C. A study of *Pycnanthemum* (Labiatae). Cal. Publ. Bot. **20**: 195–240. *1 f.* 10 Ap 1943.

Grout, A. J. Note on *Hypopterygium.* Bryologist **46**: 24. Mr [10 My] 1943.

Harper, F. *Quercus incana* Bartram. Bartonia 22: 3. 7 My 1943.

Hitchcock, C. L. The xerophyllous species of *Philadelphus* in Southwestern North America. Madroño 7: 35–56. *f. 1.* Ap 1943.

Hopkins, M. & Waterfall, U. T. Notes on Oklahoma plants. Rhodora **45**: 113–117. 10 Ap 1943.

Howell, J. T. Marin County miscellany—I. Leafl. West. Bot. **3**: 225–229. 30 Ap 1943.

Howell, J. T. New Californian localities for *Pachystima.* Leafl. West. Bot. **3**: 232. 30 Ap 1943.

Howell, J. T. New varieties of western plants—III. Leafl. West. Bot. **3**: 230–232. 30 Ap 1943.

Howell, J. T. *Sibara* on Cedros Island. Leafl. West. Bot. **3**: 229. 30 Ap 1943.

Irénée-Marie, *Frère* Étude de la flore desmidiale de la region du Lac St. Jean. Nat. Canad. **70**: 5–19. J–F [My] 1943.

Irving, F. N. *Pteris vittata* hardy in Washington, D. C. Am. Fern Jour. **33**: 28. J–F [1 Ap] 1943.

Jepson, W. L. A flora of California 3^2: 129–144. *f. 366–451.* Univ. Cal., Berkeley. 5 My 1943.

Johnston, I. M. Noteworthy species from Mexico and adjacent United States, I. Jour. Arnold Arbor. **24**: 227–236. Ap 1943.

Jones, G. N. & Jones, F. F. A revision of the perennial species of *Geranium* of the United States and Canada. Rhodora **45**: 5–26. 16 Ja 1943.

Kearney, T. H. & Peebles, R. H. *Gilia multiflora* Nutt. and its nearest relatives. Madroño 7: 59–63. Ap 1943.

Lemon, P. C. *Carex flexuosa* in Minnesota. Rhodora **45**: 167. 10 Ap 1943.

León, *Frère* Contribution a l'étude des palmiers de Cuba. VII. Nouveautés dans les palmiers royaux de Cuba oriental. Mem. Soc. Cubana Hist. Nat. **17**: 1–14. *pl. 1–3.* 3 Ap 1943.

Ley, A. A taxonomic revision of the genus *Holodiscus* (Rosaceae). Bull. Torrey Club **70**: 275–288. *f. 1–11.* 1 My 1943.

Little, E. L. Homonyms among names of trees and fossil plants. Jour. Wash. Acad. **33**: 130–135. 15 My 1943.

Little, E. L. Notes on the nomenclature of *Carya* Nutt. Am. Midl. Nat. **29**: 493–508. Mr [Ap] 1943.

Lundell, C. L. (and collaborators). New vascular plants from Texas, Mexico and Central America. Am. Midl. Nat. **29**: 469–492. *f. 1–2.* Mr [Ap] 1943.

McClintock, E. & Epling, C. A review of the genus *Monarda* (Labiatae). Cal. Pub. Bot. **20**: 147–194. *f. 1–16.* 19 N 1942.

Maguire, B. A monograph of the genus *Arnica.* Brittonia **4**: 386–527. *f. 1–101.* Mr [10 Ap] 1943.

Merrill, E. D. & Perry, L. M. Plantae Papaunae Archboldianeae, XII. Jour. Arnold Arb. **24**: 207–217. Ap 1943.

Moore, H. E. A revision of the genus *Geranium* in Mexico and Central America. Contr. Gray Herb. 146: 1–108. *pl. 1–5.* 24 My 1943.

Moran, R. A revision of *Dudleya,* subgenus *Stylophyllum*—III. Desert **15**: 24–28. *f. 5–8.* F [Ap], IV. **15**: 40–44. *f. 8–10.* Mr [My] 1943.

Ogden, E. C. The broad-leaved species of *Potamogeton* of North America north of Mexico. Rhodora **45**: 57–105. *pl. 746–748.* 18 Mr 1943, 119–163. 10 Ap 1943, 171–214. *f. 14–16.* My 1943.

Osorio Tafall, B. F. Notas sobre algunos Dinoflagelados planctonicos marinos de México, con descripcion de nuevas especies. An. Es. Nac. Cien. Biol. [Mexico] **2**: 435–447. *pl. 34–36.* 25 D 1942.

Pease, A. S. *Polygonum puritanorum* in Maine. Rhodora **45**: 215. My 1943.

Rollins, R. C. Generic revisions in the Cruciferae: *Halimolobos.* Contr. Dudley Herb **3**: 241–265. *pl. 55–57.* 10 My 1943.

Ruiz Leal, A. Observaciones sobre *Portulaca echinosperma.* Rev. Arg. Agron. **10**: 59–66. *f. 1–4.* Mr 1943.

St. John, H. Distribution of *Ophioglossum* on Islands of the Pacific Ocean. Bishop Mus. Occ. Pap. **17**: 177–182. *f. 1, 2.* 17 Mr 1943.

Sandwith, N. Y. New and noteworthy Polypetalae from British Guiana. Jour. Arnold Arb. **24**: 218–226. Ap 1943.

Sandwith, N. Y. *Ribes valdivianum.* Curt. Bot. Mag. **144**: *pl. 9647.* F 1943.

Santos, J. V. New grasses from the Philippines and South India. Jour. Wash. Acad. **33**: 135–140. *f. 1–3.* 15 My 1943.

Schornherst, R. O. Phytogeographic studies of the mosses of northern Florida. Am. Midl. Nat. **29**: 509–532. Mr [Ap] 1943.

Schweinfurth, C. A new *Galeandra* from Peru. Am. Orchid Soc. Bull. **11**: 429–431. *pl. 12.* 5 My 1943.

Senn, H. A. *Caltha natans* in Canada. Rhodora **45**: 214, 215. My 1943.

Setchell, W. A. & Mason, L. R. *Goniolithon* and *Neogoniolithon:* two genera of crustaceous coralline algae. Proc. Nat. Acad. **29**: *87–92.* Mr–Ap 1943.

Setchell, W. A. & Mason, L. R. New or little known crustaceous corallines of Pacific North America. Proc. Nat. Acad. **29**: 92–97. Mr–Ap 1943.

Shanks, R. E. & Goodum, R. H. Notes on the flora of Monroe County, New York. Proc. Rochester Acad. **8**: 299–331. *f. 1–12.* 27 Ap 1943.

Smith, A. C. Taxonomic notes on the Old World species of Winteraceae. Jour. Arnold Arbor. **24**: 119–164. *f. 1–16.* Ap 1943.

Smith, G. M. & Hollenberg, G. J. On some Rhodophyceae from the Monterey Peninsula, California. Am. Jour. Bot. **30**: 211–222. *f. 1–30.* Ap 1943.

Stehlé, H. Catalogue des cryptogames vasculaires des Antilles françaises. Carib. Forester 4: 83–89. Ja 1943.

Turrill, W. B. *Styrax officinalis.* Curt. Bot. Mag. **144**: *pl. 9653*. F 1943.

Weatherby, C. A. The range of *Notholaena delicatula.* Am. Fern Jour. **23**: 27. Ja–Mr [1 Ap] 1943.

Wherry, E. T. Variation in *Phlox floridana.* Bartonia 22: 1, 2. *pl. 1.* 7 My 1943.

Wiggins, I. L. Two new plants from the San Felipe desert, Baja California, Mexico. Contr. Dudley Herb. **3**: 285–288. *pl. 65.* 10 My 1943.

Wiggins, I. L. & Rollins, R. C. New and noteworthy plants from Sonora, Mexico. Contr. Dudley Herb **3**: 266–284. *pl. 58–64.* 10 My 1943.

Wood, C. E. *Euphorbia serpyllifolia* and *Aegilops cylindrica* in Pennsylvania. Bartonia 22: 5. 7 My 1943.

MORPHOLOGY
(including anatomy, and cytology in part)
(See also under Genetics: **Sinnott & Franklin**)

Artschwager, E. Contribution to the morphology and anatomy of guayule (*Parthenium argentatum*). U. S. D. A. Tech Bull. 842: 1–33. *pl. 1–23* + *f. 1–18.* Ap 1943.

Bates, J. C. Varietal differences in anatomy of cross-sections of wheat grains. Bot. Gaz. **104**: 490–493. *f. 1–10.* 31 Mr 1943.

Camp, W. H. & Gilly, C. L. Polypetalous forms of *Vaccinium.* Torreya **42**: 168–173. *f. 1.* N–D 1942 [24 Ap 1943].

Crafts, A. S. Vascular differentiation in the shoot apex of *Sequoia sempervirens.* Am. Jour. Bot. **30**: 110–121. *f. 1–36.* 31 Mr 1943.

Croizat, L. The cactus and its body. Cactus & Succ. Jour. **15**: 37–42. *f. 1–20.* Mr 1943.

Cross, G. L. A comparison of the shoot apices of the *Sequois.* Am. Jour. Bot. **30**: 130–142. *f. 1–15.* 31 Mr 1943.

Curtis, J. T. Germination and seedling development in five species of *Cypripedium* L. Am. Jour. Bot. **30**: 199–206. *f. 1–31.* Ap 1943.

Esau, K. Origin and development of primary vascular tissues in seed plants. Bot. Rev. **9**: 125–206. Mr 1943

Esau, K. Vascular differentiation in the vegetative shoot of *Linum.* II. The first phloem and xylem. Am. Jour. Bot. **30**: 248–255. *f. 1–9.* Ap 1943.

Johnson, E. A study of flower initiation and development in the orchid *Cattleya pinole.* Am. Orchid Soc. Bull. **11**: 422–425. *f. 1–5.* 5 My 1943.

Long, E. M. Developmental anatomy of the fruit of the Deglet Noor date. Bot. Gaz. **104**: 426–436. *f. 1–19.* 31 Mr 1943.

McIntyre, W. G. & Chrysler, M. A. The morphological nature of the photosynthetic organs of *Orchyllium endresii* as indicated by their vascular structure. Bull. Torrey Club **70**: 252–260. *f. 1–10.* 1 My 1943.

Preston, R. J. Anatomical studies of the roots of juvenile lodge-pole pine. Bot. Gaz. **104**: 443–448. *f. 1–8.* 31 Mr 1943.

Scott, F. M. Survey of anatomy, ergastic substances, and nuclear size in *Echinocystis macrocarpa* and *Cucurbita pepo.* Bot. Gaz. **104**: 394–408. *f. 1–23.* 31 Mr 1943.

Thomson, B. F. Development of sorus and prothallium of *Acrophorus stipellatus.* Bot. Gaz. **104**: 437–442. *f. 1–29.* 31 Mr 1943.

PLANT PHYSIOLOGY

(See also under Mycology: **Nickerson & Thimann; Wynd**)

Addicott, F. T. Pollen germination and pollen tube growth, as influenced by pure growth substances. Plant Physiol. **18:** 270–279. Ap 1943.

Anderson, D. B. & Kerr, T. A note on the growth behavior of cotton bolls. Plant Physiol. **18:** 261–269. *f. 1–7.* Ap 1943.

Bonner, J. Effects of application of thiamine to *Cosmos.* Bot. Gaz. **104:** 475–479. 31 Mr 1943.

Bloch, R. Polarity in plants. Bot. Rev. **9:** 261–310. My 1943.

Burkholder, P. R. Vitamin deficiencies in yeasts. Am. Jour. Bot. **30:** 206–211. *f. 1–2.* Ap 1943.

Day, D. Growth of excised tomato roots in agar with thiamine plus pyridoxine, nicotinamide or glycine. Am. Jour. Bot. **30:** 150–156. *f. 1–2.* 31 Mr 1943.

Emerson, R. & Lewis, C. M. The dependence of the quantum yield of *Chlorella* photosynthesis on wave length of light. Am. Jour. Bot. **30:** 165–178. *f. 1–7.* Ap 1943.

Eyster, H. C. Osmosis and osmotic pressure. Bot. Rev. **9:** 311–324. My 1943.

Frazier, J. C. Amount, distribution and seasonal trend of certain organic reserves in the root system of field bindweed, *Convolvulus arvensis* L. Plant Physiol. **18:** 167–184. *f. 1–6.* Ap 1943.

Freeland, R. O. The American mistletoe with respect to chlorophyll and photosynthesis. Plant Physiol. **18:** 299–302. *f. 1.* Ap 1943.

Gortner, R. A. The plant proteins. Wallerstein Comm. **6**[17]: 33–42. *f. 1–4.* Ap 1943.

Graham, E. R. & Albrecht, W. A. Nitrate absorption by plants as an anion exchange phenomenon. Am. Jour. Bot. **30:** 195–198. *pl. 1, 2 + f. 1.* Ap 1943.

Greulach, V. A. Photoperiodic aftereffects in *Ipomoea.* Ohio Jour. Sci. **42:** 65–73. *f. 1.* Mr 1943.

Kozlowski, T. T. Transpiration rates of some forest tree species during the dormant season. Plant Physiol. **18:** 252–260. *f. 1–2.* Ap 1943.

Kramer, P. J. Amount and duration of growth of various species of tree seedlings. Plant Physiol. **18:** 238–251. *f. 1–4.* Ap 1943.

McNair, J. B. Hydrophytes, xerophytes and halophytes and the production of alkaloids, cyanogenetic and organic compounds. Lloydia **6:** 1–17. Mr [My] 1943.

Magistad, O. C. *et al.* Effect of salt concentration, kind of salt, and climate on plant growth in sand cultures. Plant Physiol. **18:** 151–166. *f. 1–9.* Ap 1943.

Moyer, L. S. & Fishman, M. M. The chlorophyll-protein complex. II. Species relationships in certain legumes as shown by electric mobility curves. Bot. Gaz. **104:** 449–454. *f. 1–4.* 31 Mr 1943.

Noggle, G. R. & Wynd, F. L. Effects of vitamins on germination and growth of orchids. Bot. Gaz. **104:** 455–459. 31 Mr 1943.

Northen, H. T. Relationship of dissociation of cellular proteins by incipient drought to physiological processes. Bot. Gaz. **104:** 480–485. *f. 1.* 31 Mr 1943.

Osterhout, W. J. V. Pacemakers in *Nitella* III. Electrical alternans. Jour. Gen. Physiol. **26:** 457–465. *f. 1–8.* 20 My 1943.

Sullivan, J. T. & Chilton, S. J. P. The composition of white clover leaves as affected by rust and by sulphur. Phytopathology **33:** 401, 402. My 1943.

Swanson, C. P. Differential sensitivity of prophase pollen tube chromosomes

to x-rays and ultraviolet radiation. Jour. Gen. Physiol. **26**: 485–494. *pl. 4.* 20 My 1943.

Went, F. W. Transplantation experiments in peas. III. Bot. Gaz. **104**: 460–474. 31 Mr 1943.

Withrow, A. P., Withrow, R. B. & Biebel, J. P. Inhibiting influence of the leaves on the photoperiodic response of Nobel spinach. Plant Physiol. **18**: 294–298. *f. 1–2.* Ap 1943.

Withdrow, A. P. & Withrow, R. B. Translocation of the floral stimulus in *Xanthium.* Bot. Gaz. **104**: 409–416. *f. 1–3.* 31 Mr 1943.

Wolf, F. T. & Shoup, C. S. The effects of certain sugars and amino acids upon the respiration of *Allomyces.* Mycologia **35**: 192–200. 5 Ap 1943.

GENETICS
(including cytogenetics)

(See also under Taxonomy: **Camp & Gilly**; under Plant Physiology: **Swanson**)

Anderson, E. & Hubricht, L. The histological basis of a specific difference in leaf texture. Am. Nat. **77**: 285–287. My 1943.

Ausemus, E. R. Breeding for disease resistance in wheat, oats, barley and flax. Bot. Rev. **9**: 207–260. Ap 1943.

Baker, R. E. Induced polyploid periclinial chimeras in *Solanum tuberosum.* Am. Jour. Bot. **30**: 187–195. *f. 1–32.* Ap 1943.

Brumfield, R. T. Cell-lineage studies in root meristems by means of chromosome rearrangements induced by x-rays. Am. Jour. Bot. **30**: 101–110. *f. 1–18.* 31 Mr 1943.

Caldwell, R. M. & Compton, L. E. Complementary lethal genes in wheat causing a progressive lethal necrosis of seedlings. Jour. Hered. **34**: 67–70. *1 pl.* Mr [My] 1943.

Cave, M. S. & Bradley, M. V. Alteration of chromosome number in *Miersia chilensis.* Am. Jour. Bot. **30**: 142–149. *f. 1–18.* 31 Mr 1943.

Clark, F. J. Cytological and genetic studies of sterility in inbred and hybrid maize. Conn. Exp. Sta. Bull. 465: 703–726. *f. 1–15.* S 1942.

Ownbey, M. & Weber, W. A. Natural hybridization in the genus *Balsamorhiza.* Am. Jour. Bot. **30**: 179–187. *f. 1–20.* Ap 1943.

Sinnott, E. W. & Franklin, A. H. A developmental analysis of the fruit in tetraploid as compared with diploid races of cucurbits. Am. Jour. Bot. **30**: 87–94. 31 Mr 1943.

Smith, H. E. Polyploidy in *Sedum pulchellum*—II. Stomatal size and frequency. Bull. Torrey Club **70**: 261–264. *f. 1.* 1 My 1943.

Smith, H. H. Studies on induced heteroploids of *Nicotiana.* Am. Jour. Bot. **30**: 121–130. *f. 1–33.* 31 Mr 1943.

Thompson, W. P., Britten, E. J. & Harding, J. C. The artificial synthesis of 42-chromosome species resembling common wheat. Canad. Jour. Res. **21**: 134–144. *pl. 1.* Ap 1943.

Wright, S. An analysis of local variability of flower color in *Linanthus Parryae.* Genetics **28**: 139–156. Mr 1943.

MYCOLOGY AND PHYTOPATHOLOGY

(See also under Plant Physiology: **Sullivan & Chilton; Wolf & Shoup**)

Benedek, T. Unilateral stimulation of *Microsporum Andouini* by a new species of bacillus. Mycologia **35**: 222–242. *f. 1–7.* 5 Ap 1943.

Bingham, R. T. & Ehrlich, J. A *Dasyscypha* following *Cronartium ribicola* on *Pinus monticola.* I. Mycologia **35**: 95–111. *f. 1–2.* 1 F 1943. II. 294–311. *f. 1–2.* 1 Je 1943.

Black, L. M. Some relationships between potato yellow-dwarf virus and the clover leaf hopper. Phytopathology **33**: 363–371. My 1943.

Bose, S. R. Moisture-relation as a determinant factor in the transformation of the basidia of certain Polyporaceae. Mycologia **35**: 33–46. *f. 1–8.* 1 F 1943.

Cooke, W. B. Some Basidiomycetes from Mount Shasta. Mycologia **35**: 277–293. 1 Je 1943.

Darley, E. F. & Christensen, C. M. An unusual sporophore of *Trametes suaveolens* produced on artifically inoculated wood. Phytopathology **33**: 328–330. *f. 1.* Ap 1943.

Dimock, A. W. & Osborn, J. H. An alternaria disease of *Zinnia*. Phytopathology **33**: 372–381. *f. 1–3.* My 1943.

Dix, W. L. The Cladoniae of Pennsylvania. Bartonia 22: 32–62. *pl. 2.* 7 My 1943.

Drechsler, C. A new nematode-capturing *Dactylella* and several related Hyphomycetes. Mycologia **35**: 339–362. *f. 1–4.* 1 Je 1943.

Drechsler, C. A new non-helicoid bisporous *Helicocephalum* parasitizing nematode eggs. Mycologia **35**: 134–141. *f. 1.* 5 Ap 1943.

Drechsler, C. Two species of *Pythium* occurring in southern states. Phytopathology **33**: 261–299. *f. 1–16.* Ap 1943.

Ellett, C. W. Leaf blight of corn. Phytopathology **33**: 407, 408. My 1943.

Foster, H. H. Resistance in the genus *Nicotiana* to *Phytophthora parasitica Dastur* var. *nicotianae* Tucker. Phytopathology **33**: 403, 404. My 1943.

Greene, H. C. Notes on Wisconsin parasitic fungi. II. Trans. Wis. Acad. **34**: 83–98. 1942 [Ap 1943].

Grodsinsky, L. & Jenkins, A. E. *Sphaceloma Murrayae* en diversas especies de *Salix*. Rev. Arg. Agron. **10**: 55–58. *pl. 1* + *f. 1.* Mr 1943.

Hagelstein, R. Notes on Mycetozoa—VII. Mycologia **35**: 363–380. 1 Je 1943.

Hahn, G. G. Blister-rust relations of cultivated species of red currants. Phytopathology **33**: 341–353. My 1943.

Hardison, J. R. & Sprague, R. A leaf spot of grasses caused by a new species of *Phleospora*. Mycologia **35**: 185–188. *f. 1–2.* 5 Ap 1943.

Hart, H. Stem rust on *Triticum timopheevi*. Phytopathology **33**: 335–337. *f. 1.* Ap 1943.

Herre, A. W. C. T. Two new species of lichens and new records for Washington State and North Carolina. Proc. Biol. Soc. Wash. **56**: 17–20. 25 F 1943.

Jenkins, A. A. Leaf spot on *Terminalia arjuna*. Phytopathology **33**: 404, 405. *f. 1.* My 1943.

Jenkins, A. E. & Bitancourt, A. A. Gouirand and Bergeron's treatment of *Sphaceloma ampelinum*. Mycologia **35**: 272–276. *f. 1.* 1 Je 1943.

Kung-Hsiang, Lin Convex gum, a new disease of *Citrus* in China. Phytopathology **33**: 394–397. *f. 1.* My 1943.

Linford, M. B. Influence of plant populations upon incidence of pineapple yellow spot. Phytopathology **33**: 408–410. My 1943.

McKeen, C. D. A study of some factors affecting the pathogenicity of *Verticillium albo-atrum* R. & B. Canad. Jour. Res. C **21**: 95–117. Mr 1943.

McKinney, H. H. Studies on genotypes of tobacco resistant to the common-mosaic virus. Phytopathology **33**: 300–313. Ap 1943.

McLean, R. A. Observations on *Cercospora* leaf spot of tobacco and the question of varietal resistance. Phytopathology **33**: 354–362. *f. 1–2.* My 1943.

Mead, H. W. Seed-borne moulds of barley. Wallerstein Comm. **6**[17]: 26–32. *illust.* Ap 1943.

Meredith, C. H. The effect of soil and chemical mixtures on the growth of *Fusarium oxysporum cubense.* Phytopathology **33:** 398–400. My 1943.

Middleton, J. T. Phytophthora rot of belladonna. Bull. Torrey Club **70:** 244–251. *f. 1–8.* 1 My 1943.

Middleton, J. T. The taxonomy, host-range and geographic distribution of the genus *Pythium.* Mem. Torrey Club **20**[1]**:** 1–171. *f. 1–17.* 22 Ap 1943.

Miller, J. H. & Burton, M. G. Study of *Bagnisiopsis* species on the Melastomaceae. Mycologia **35:** 312–334. *f. 1–23.* 1 Je 1943.

Mundkur, B. B. & Kheswalla, K. F. *Dasturella*—a new genus of Uredinales. Mycologia **35:** 201–206. *f. 1–5.* 5 Ap 1943.

Nickerson, W. J. & Thimann, K. V. The chemical control of conjugation in *Zygosaccharomyces.* II. Am. Jour. Bot. **30:** 94–101. 31 Mr 1943.

Overholts, L. O. Mycological notes for 1939–40. Mycologia **35:** 243–254. *f. 1–7.* 5 Ap 1943.

Presley, J. T. & King, C. J. A description of the fungus causing cotton rust and a preliminary survey of its hosts. Phytopathology **33:** 382–389. *f. 1–3.* My 1943.

Shear, C. L. Conserving names of fungi. Mycologia **35:** 267–271. 1 Je 1943.

Singer, R. Type studies on Basidiomycetes. II. Mycologia **35:** 142–163. 5 Ap 1943.

Skok, J. Defoliation of tomato plant as a response to gaseous emanations from the fruit. Bot. Gaz. **104:** 486–489. 31 Mr 1943.

Slagg, C. M. & Wright, E. Diplodia blight in coniferous seedbeds. Phytopathology **33:** 390–393. My 1943.

Sprague, R. The status of *Septoria Alopecuri* and some related species. Mycologia **35:** 259–263. *f. 1.* 1 Je 1943.

Starr, M. P. *et al* Growth of phytopathogenic bacteria in a synthetic asparagin medium. Phytopathology **33:** 314–318. Ap 1943.

Stevens, N. E. & Thompson, N. F. Factors influencing injury to cranberry plants during flooding. Trans. Wis. Acad. **34:** 73–81. 1942 [Ap 1943].

Stuntz, D. E. & Seliskar, C. E. A stem canker of dogwood and madrona. Mycologia **35:** 207–221. *f. 1–6.* 5 Ap 1943.

Sumstine, D. R. New stations for two fungi. Mycologia **35:** 264–266. *f. 1.* 1 Je 1943.

Tapke, V. F. Physiologic races of *Ustilago nigra.* Phytopathology **33:** 324–327. Ap 1943.

Vecchierello, H. The Myxomycetes of Cattaraugus County, N. Y. Sci. Stud. St. Bonaventure Coll. **11**[3]**:** 24–26. Mr 1943.

Weimer, J. L. A *Botrytis* disease of Lupines. Phytopathology **33:** 319–323. *f. 1.* Ap 1943.

Whetzel, H. H. A monograph of *Lambertella,* a genus of brown-spored inoperculate Discomycetes. Lloydia **6:** 18–52. *pl. 1–6 + f. 1–7.* Mr [My] 1943.

Whetzel, H. H. The spermodochidium, an unusual type of spermatial fruit-body in the Ascomycetes. Mycologia **35:** 335–338. 1 Je 1943.

Wynd, F. L. Chlorosis in Sudan grass. Plant Physiol. **18:** 303–305. Ap 1943.

Yarwood, C. E. Association of thrips with powdery mildews. Mycologia **35:** 189–191. 5 Ap 1943.

Zundel, G. L. Notes on the Ustilaginales of the world. III. Mycologia **35:** 164–184. *f. 1–4.* 5 Ap 1943.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 5, pp. 449–456 SEPTEMBER, 1943

THE GERMINATION CAPACITY OF MAIZE POLLEN HAVING ABERRANT NUCLEI[1]

FRANCES CLARK BEARD

INTRODUCTION

As a result of the action of the gene *dv*, divergent spindle, pollen grains of *Zea mays* may have unusual morphological organization. The frequency of their occurrence is high enough to test the germination capacity. Owing to the configuration of the meiotic division spindles in *dv* plants, multinucleate microspores and pollen grains are developed. At the time of the division to form the tube and generative nuclei, multinucleate spores appear normal when the complete chromosome complement is present even though the chromosomes are incorporated in several nuclei and are separated by nuclear membranes. It has been thought that the germination of a pollen grain is regulated by the action of the tube nucleus (vegetative nucleus), and it was with reference to this concept that the germination of the multinucleate pollen grains was tested.

Evidence will be presented that pollen grains of *dv* plants may have the chromosome complement of the vegetative cell distributed among several nuclei. The germination capacity of such pollen grains was of particular interest. In a preliminary account (Clark 1942) it was reported that pollen grains having both more and less than the normal number of nuclei were able to germinate during the period of time allowed for germination.

The recessive mutant *dv* found in maize (Clark 1940) is limited in action to the time of the divisions of the microsporocytes. Except for characteristic pollen abortion, the plants are indistinguishable from normal (*Dv*), and megasporocyte development is normal. When the recessive gene is present in the homozygous condition, the spindle of the first meiotic division diverges at the polar regions rather than having the characteristic convergence of the spindle fibers. The chromosomes follow the form of the spindle during anaphase and thus diverge from each other. At telophase several nuclei are formed, and one or more chromosomes are incorporated in each nucleus. Each cell at the end of the first meiotic division has the normal chromosome complement characteristic of such cells although the chromosomes are distributed among several nuclei. As a result of the multinucleate condition at the end of the first meiotic division, a multi-spindle condition is developed

[1] The writer wishes to express her appreciation for the use of the facilities of the Genetics Department, Connecticut Agricultural Experiment Station, New Haven, Connecticut.

[The BULLETIN for July (70: 335–448) was issued July 12, 1943]

in the second meiotic division with each nucleus forming its own spindle. The several spindles may lie parallel or at various angles to each other, and may be divergent. Thus a multinucleate condition again results at the end of the second meiotic division, and each microspore may have from few to many nuclei.

A return to the normal nuclear condition usually takes place after the first microspore division, and most of the microspores then contain a tube nucleus in the vegetative cell and a generative nucleus in the generative cell. The division of the generative nucleus to form the two sperm cells occurs in maize before anthesis and results in normal mature pollen with three nuclei: a tube nucleus of the vegetative cell and two sperm nuclei (fig. 1).

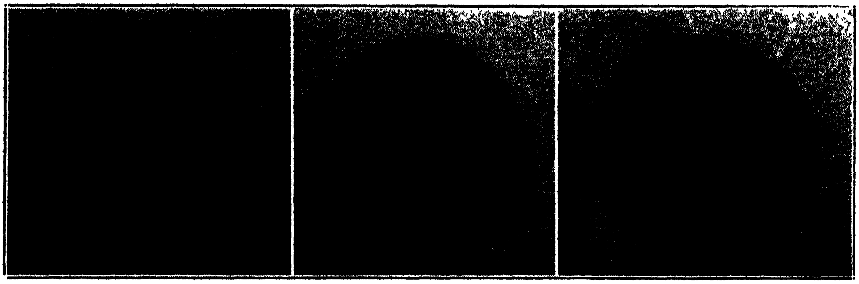
In about 94 per cent of the microspores of *dv* plants there is a return to the normal nuclear condition after the first division. These microspores may or may not develop into functional pollen grains depending upon whether or not a complete chromosome complement is present. The pollen abortion (determined by counting the number of small grains and grains having no starch relative to large, normally filled pollen) is variable among different samples taken from the same or different *dv* plants, but may be as high as 90 per cent.

OCCURRENCE OF MULTINUCLEATE POLLEN GRAINS

In six per cent of the male gametophytes there continues to be a multinucleate condition after the first microspore division, and it is from these spores that multinucleate pollen grains were to be expected. The spindle of the first microspore division in spores that will have multinucleate vegetative and generative cells gives evidence for the chromosome distribution among the several nuclei.

When the microspores were examined at this stage, some of the spores were found to have the spindle of the first microspore division diverging at one or both poles. During anaphase the chromosomes follow the form of the spindle, and thus at telophase several nuclei were present at either or both poles, the inner pole forming the nuclei or nucleus of the vegetative cell. Since the nuclei of the vegetative cell do not divide again when the generative nucleus divides, and since the chromosomes diverge from each other, it is assumed that the multinucleate vegetative cells observed in the pollen grains have resulted from the divergent spindle figures in the first microspore division.

The multinucleate spores may contain (1) more than one nucleus in the generative cell, (2) more than one nucleus in the vegetative cell, or (3) several nuclei in both the generative and vegetative cells. The counts that were made (Clark 1940) indicated that the second condition was the most frequent. The division of the generative nucleus was not observed.



FIGS. 1, 2, 3. Photographs of pollen stained with acetocarmine. About 350 ×. FIG. 1. Pollen grain with the normal organization. Two small sperm cells (long, narrow) and one vegetative cell containing the larger nucleus (tube nucleus) having a prominent nucleolus were present. FIG. 2. Pollen grain with two nuclei, each with a definite nucleolus. There was no division to form the two sperm cells from the generative cell. FIG. 3. Pollen grain with only one nucleus, indicating a failure of the microspore divisions.

However, pollen grains having the nuclear constitution shown in figure 4 indicate that this division will occur in male gametophytes whose chromosome complement in the vegetative cell is included in more than one nucleus.

The nuclei in the pollen grain may be observed after staining and clearing either fresh or fixed pollen. Table 1 gives counts of the number of nuclei in individual pollen grains obtained from two *dv* plants. The pollen grains with three nuclei, two sperm nuclei and one tube nucleus, represent the normal condition. The presence of only one or two nuclei of the type shown in figures 2 and 3 suggests that the microspore divisions failed to take place. When a single nucleus is present as in figure 3, there may have been no first division in the microspore to form the vegetative and generative nuclei. When two nuclei were found as in figure 2, no division of the generative nucleus had taken place to form the two sperm cells. The evidence for this lies in a consideration of the size of the nuclei and the character of the nucleoli present.

Since pollen grains in the category with two nuclei (table 1) all had a good nucleolus in each nucleus, it was evident that one was the vegetative nucleus and one the generative nucleus. Had they been pollen grains with

TABLE 1. *Number of pollen grains with the indicated nuclei in mature pollen of dv/dv plants.*

Plant	Distribution of nuclei				Total*
	2 tube 2 sperm	1 tube 2 sperm	Only 2 nuclei	Only 1 nucleus	
148–8	0	73	29	10	112
166–13	1	332	7	18	358
Total	1	405	36	28	470

* Not including small pollen grains and those devoid of starch.

two nuclei in the vegetative cell, and with the chromosomes distributed among the two nuclei, the nucleoli would not have been organized. McClintock (1934) has shown that the presence of chromosome 6, the satellite chromosome in maize, is essential for the organization of a nucleolus. A nucleus deficient for chromosome 6 does not have the nucleolar material organized into a single nucleolus, and likewise a nucleus with certain deficiencies does not have an organized nucleolus. It is evident from the vegetative nuclei shown in figure 4 that neither of the two nuclei has a nucleolus such as is shown by the nucleus of the vegetative cell in figure 1.

Therefore, the conclusion may be drawn that the nuclei in the pollen grain shown in figure 2 each have the haploid chromosome complement, having a nucleolus in each nucleus, and that the haploid complement is divided between the two nuclei in the vegetative cell of the pollen grain shown in figure 4. The size of a nucleus gives some indication of the number of chromosomes it contains. The nuclei of the vegetative cell in figure 4

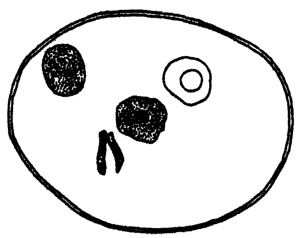


FIG. 4. Camera lucida drawing of a pollen grain having two tube nuclei (the larger nuclei) and two sperm nuclei. The non-stippled circles indicate the position of the germ pore. About 400 ×.

were relatively smaller than the nucleus of the vegetative cell of the pollen grain shown in figure 1. This also shows that the chromosome complement in the binucleate vegetative cells was divided among the two nuclei.

The determination of the germination capacity of pollen grains with more and less than the normal three nuclei was undertaken. These types in table 1 were 13.8 per cent of the total counted.

GERMINATION OF MULTINUCLEATE POLLEN GRAINS

Corn pollen requires more rigidly controlled conditions for germination on artificial media than pollen from liliaceous plants. Recently, Bair and Loomis (1941) have reported an agar medium on which corn pollen will germinate. In the present tests, however, it was desired to allow the pollen to germinate under conditions closely approaching the normal.

Small pieces of corn silks, cut before emerging beyond the husks or when protected by ear shoot bags, approximately one inch long were placed in small Petri dishes or in watch glasses. Pollen to be tested was dusted on

the silks and allowed to remain from 30 minutes to one hour. With a longer germination time, the germ tubes of many pollen grains had penetrated the silk as well as the silk hairs, and the nuclei had migrated into the tubes too far to be adequately observed. Many pollen grains adhere to the silk hairs, and the germ tubes then penetrate the hair before entering the main part of the silk, although the germ tube may penetrate the silk without first entering a silk hair. After the pollen tubes have penetrated the silk and started growing down it, along a vascular bundle, it is difficult to determine the position of one particular tube and distinguish its nuclei. During the time allowed for the germination test, the germ tubes usually had penetrated the silk hairs, and the nuclei were still in the pollen grain or were just beginning to enter the tube.

After the time allowed for this germination test, the silks were fixed in an acetic acid—alcohol mixture (1:3) and stained with acetocarmine, clearing being done with chloral hydrate. During the fixing and staining,

TABLE 2. *Nuclei in germinated pollen grains of dv plants.*

Plant	Number of nuclei				Total
	>3	3	2	1	
137–6	0	131	3	2	136
137–6	1	73	3	0	77
166–8	0	134	0	3	137
210–5	1	157	4	0	162
Total	2	495	10	5	512

pollen grains that had germinated remained well attached to the silk, and some grains which did not have tubes penetrating the silk hairs were also present in the preparations. The non-germinated grains which still adhered to the silks after fixation included about 25 per cent of the total pollen grains present on the silk.

The pollen grains that had germinated were classified according to the number of nuclei present, and the results are given in table 2. The germination of pollen grains with less than three nuclei and more than three nuclei is illustrated in figure 5.

The number of pollen grains representing types with other than the normal three nuclei in table 1 consisted of 13.8 per cent of the total counted. In table 2, the number of such pollen grains that had germinated amounted to 3.3 per cent. It is likely that the time allowed for the experiment was too short to test adequately the germination capacity of all the aberrant types even though they appeared normal with respect to walls, starch content, and size.

The two pollen grains containing more than three nuclei listed in table 2 possessed two tube nuclei and three sperm nuclei, and two tube nuclei and

FIG. 5. Semidiagrammatic camera lucida drawings of germinated pollen. About 400 ×. A. Pollen grain with one nucleus. B. Pollen grain with two nuclei. C. Pollen grain with four nuclei—two tube nuclei in the vegetative cell and two sperm cells (upper).

two sperm nuclei, respectively. Among the pollen grains which had not germinated, other multinucleate types were found as shown in table 3. In all of these the morphological development of the grain was normal except for the nuclear constitution.

TABLE 3. *Nuclei in aberrant non-germinated pollen grains. Normal pollen grains have one tube and two sperm nuclei.*

Tube nuclei	Sperm nuclei	Frequency of occurrence
1	0	3
1	3?	1
2	0	7*
2	2	2
2	2 or 3	1
3	2	2

* For convenience these are listed in this table, although this type is the same as the two-nuclei category of tables 1 and 2 and figures 2 and 5B.

DISCUSSION

The separation of the chromosome complement of the vegetative cell into more than one nucleus does not affect the functioning of the complement as a whole during the germination of a pollen grain. The results also indicated that in the absence of a characteristic tube nucleus (when only one or two nuclei were present as in figures 2 and 3), germination took place during the period of observation. The problems of whether or not tubes from such pollen grains would continue to grow, given a longer time, and whether or not fertilization or an initiation of ovule development would take place remain unanswered.

Chamberlain (1897), Smith (1898), and Fullmer (1899) have reported observing microspores with several tube nuclei, and also male gametophytes with multinucleate generative cells. It was not determined whether the division of the generative nucleus took place in these aberrant male gametophytes. Microspores deficient for part of the chromosome complement and defective in wall formation were studied by Barber (1941, 1942) and Sax (1942). They conclude that when a deficient microspore remains partially attached to a normal microspore, or when the two contain deficiencies that are complementary, normal development takes place. They assume that the gene products which control the development of the microspore are unable to diffuse through the cell wall to direct the normal development of the unattached deficient microspores.

A tube nucleus with the normal chromosome complement may control the germination of a pollen grain even though the sperm nuclei may be deficient in chromosome number. McClintock (1938) and Rhoades (1940) have explained the transmission of deficient male gametes in this way.

If there were an unequal distribution of chromosomes in the first microspore division of *dv* plants, there could result a vegetative cell with at least the normal chromosome complement, in one or more nuclei, and a deficient generative cell. To test whether any deficient male gametes were transmitted, pollen from *dv/dv* plants was placed on silks of normal plants and the chromosome numbers of 82 plants in the progeny were determined. Seventy-nine plants were found with the normal chromosome complement (20), and three were heteroploid plants. One of the three was a triploid, the second a monosomic (19 chromosomes), and the third had a complete deficiency for the long arm of chromosome 10, leaving the short arm a telocentric fragment similar to the chromosome 5 found by Rhoades (1940). Although suggestive of transmission of deficient male gametes, the counts are too few to justify a positive statement.

Pollen from plants homozygous for *dv* may give rise to a low frequency of aneuploid progeny. Haploids could be expected if pollen tubes from grains containing only one or two nuclei should grow long enough to penetrate the ovule and initiate ovule development.

CONCLUSIONS

1. Evidence is presented from *dv* plants of maize that male gametophytes are able to develop a normal morphological organization when the chromosome complement of the vegetative and generative cells is contained in more than one nucleus.

2. A pollen grain with a multinucleate vegetative cell is capable of forming a normal germination tube which penetrated the silk and continued to grow during the time allowed for a germination test, one hour.

3. Pollen grains lacking the usual morphological organization of the male gametophytes, that is, those possessing only one or two nuclei, were found to be capable of forming germ tubes during the time allowed for germination.

BROOKSVALE ROAD
MT. CARMEL, CONNECTICUT

Literature Cited

Bair, R. A. & Loomis, W. E. 1941. The germination of maize pollen. Science **94**: 168.

Barber, H. N. 1941. Chromosome behavior in *Uvularia*. Jour. Genet. **42**: 223–257.

————. 1942. The pollen-grain division in the Orchidaceae. Jour. Genet. **43**: 97–103.

Chamberlain, C. J. 1897. Contribution to the life history of *Lilium Philadelphicum*; II. The pollen grain. Bot. Gaz. **23**: 423–430.

Clark, F. J. 1940. Cytogenetic studies of divergent meiotic spindle formation in *Zea mays*. Am. Jour. Bot. **27**: 547–559.

————. 1942. Preliminary investigations in *Zea mays* of the germination capacity of pollen with aberrant nuclei. Genetics **27**: 137. [Abstract].

Fullmer, E. L. 1899. The development of the microsporangia and microspores of *Hemerocallis fulva*. Bot. Gaz. **28**: 81–88.

McClintock, B. 1934. The relation of a particular chromosomal element to the development of the nucleoli in *Zea mays*. Zeits. Zellfors. & Micros. **21**: 294–328.

————. 1938. The fusion of broken ends of sister half-chromatids following chromatid breakage at meiotic anaphases. Mo. Coll. Agr. Res. Bull. 290: 1–48.

Rhoades, M. M. 1940. Studies of a telocentric chromosome in maize with reference to the stability of its centromere. Genetics **25**: 483–520.

Sax, K. 1942. Diffusion of gene products. Proc. Nat. Acad. **28**: 303–306.

Smith, W. R. 1898. A contribution to the life history of the Pontederiaceae. Bot. Gaz. **25**: 324–337.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 5, pp. 457–467 SEPTEMBER, 1943

A CYTOLOGICAL STUDY OF C–MITOSIS IN THE POLYSOMATIC PLANT SPINACIA OLERACEA, WITH COMPARATIVE OBSERVATIONS ON ALLIUM CEPA[1]

C. A. BERGER AND E. R. WITKUS

This investigation arose in the course of a comparative study[2] of prophase chromosome behavior at meiosis and polysomatic mitosis in *Spinacia oleracea*. Colchicine treatment was tried in the hope of obtaining a third type of prophase chromosome behavior in this material. Detailed cytological descriptions of the effects of this drug on cell division are few and incomplete. Most of the studies have dealt with *Allium* or *Tradescantia* and the treatment has apparently never been tried on a polysomatic plant.

The effects of colchicine on *Spinacia* were so striking and so different from the effects on *Allium* as described in the literature that it was thought necessary to make a series of experiments with *Allium* as controls. These experiments confirmed the opinion that there is a real difference in the cytological effects of colchicine treatment in *Spinacia* and in *Allium*. This interesting difference in the reaction of the two plants to the drug, together with the lack of a comprehensive cytological description of its effects on mitosis, prompted the present report.

Following the terminology of Levan (1938), mitosis under the influence of colchicine will be termed c-mitosis, and the various stages in the process will be similarly designated. In describing colchicine experiments it is necessary to distinguish three types of effects as follows. Direct effects occur while the cells are under the influence of the drug, while recovery effects persist after the direct influence of colchicine has completely disappeared and transitional effects appear in early recovery before the influence of the drug is completely removed.

The effects most commonly referred to the direct action of colchicine are the prevention of effective spindle formation and the delay in the division of the spindle attachment regions or SA-regions as they will be termed in this paper. These two effects will be classified as *primary direct effects*. In addition there are a number of *secondary direct effects,* direct because they occur during the actual treatment with the drug, secondary because their immediate cause is not the presence of colchicine but either the absence of an effective spindle, the delay in the division of the SA-region, or both of these primary direct effects.

[1] Publication of plates 1 and 2 is assisted by the Lucien M. Underwood Memorial Fund.

[2] Aided by a grant from the Penrose Fund of the American Philosophical Society.

The following are here classified as secondary direct effects. (1) Diplochromosomes, the c-pairs of Levan, two chromosomes united at a common undivided SA-region. (2) The long duration of c-metaphase, due to failure of formation of an organized spindle. (3) The extreme shortness or condensation frequently found in chromosomes at c-metaphase, owing to the additional time allowed for the action of coiling forces. (4) The formation of restitution or reversion nuclei, due to the absence of an effective spindle. (5) The variety of shapes assumed by restitution nuclei, dependent on the amount and disposition of the disorganized spindle substance. (6) Increase in cell size, due to failure of division. (7) Polyploidy, likewise due to failure of division. (8) Secondary pairing of chromosomes owing to the absence of anaphase separation of chromosomes.

MATERIAL AND METHODS

Root tips of *Spinacia oleracea* (Old Dominion variety) and of *Allium cepa* were used. Germinating seeds of *Spinacia* were treated with 0.06 per cent and 0.25 per cent solutions of colchicine for one, five, and twelve hours. They were then washed in water for a half hour and fixed immediately and at intervals of five, twenty-four, thirty-two, forty-eight, fifty-three, sixty-three, sixty-six, sixty-nine, and seventy-two hours after treatment. Root tips of *Allium* were treated with a 0.25 per cent colchicine solution for five and twelve hour periods. They were then washed in water and fixed immediately and at five and twenty-four hour intervals after treatment.

Most of the *Spinacia* material was prepared by the smear technique. The tips were fixed in three parts of absolute alcohol and one part of glacial acetic acid, and the Feulgen stain was used. Eight minutes of hydrolysis was found to be correct after the above fixation. A series of root tips were fixed in Craf fixative, and longitudinal and cross sections were cut and stained by the Feulgen technique. After fixation in the Craf solution forty-five minutes of hydrolysis was required for the Feulgen reaction. The *Allium* material was all prepared in the form of smears, some were stained with aceto-carmine and others by the Feulgen technique.

OBSERVATIONS ON ALLIUM

Our observations on the effect of colchicine on mitosis in *Allium* are in general agreement with those of Levan (1938) and Shimamura (1939) on the same material, and with those of Walker (1938) on *Tradescantia* and of Beams and King (1938) on *Triticum*. It has been possible however, to add to the details of the process of c-mitosis especially in regard to the formation of the restitution or reversion nucleus following the stoppage of mitosis at c-metaphase. These observations on *Allium* are not a complete series of experiments involving an ordered series of time treatments with increasing concentrations of colchicine. They are a selected set of experiments designed

to verify the results of other investigators with respect to those points wherein *Spinacia* apparently differs from *Allium* in the cytological response to the drug.

Description of c-Mitosis in Allium. Prophase of mitosis appears to proceed normally in the presence of colchicine. At very late prophase or prometaphase (pl. 1, fig. 1) the chromosomes reach their normal metaphase degree of contraction. They have a clearly defined SA-region and their division into chromatids is very evident. The chromatids are relationally coiled. There is no nuclear membrane present at this stage and the chromosomes are scattered in the center of the cell. In normal mitosis the chromosomes at this stage would congress upon the metaphase plate, their SA-regions would divide and anaphase separation would take place. In the presence of colchicine a well defined spindle is not formed and the metaphase stage, normally of short duration, becomes greatly lengthened extending over a period of four or five days, according to some investigators. Evidence of this prolongation of metaphase is had in the increasing number of metaphase stages found in the older preparations of a series.

During this protracted metaphase the chromosomes undergo marked changes. The relational coiling of chromatids is undone. The division of the SA-region is greatly delayed and the chromatids separate at all other points giving characteristic X-shaped configurations similar to those seen at meiotic interphase. In normal mitosis these chromosomes would be undergoing anaphase separation. Such pairs of chromosomes held together by an undivided SA-region are called diplo-chromosomes in this paper. The diplo-chromosomes in *Allium* are usually arranged around the surface of an achromatic sphere (pl. 1, figs. 2, 4) composed, according to Shimamura (1939), of a substance which normally would take part in the formation of the spindle. During c-metaphase the chromosomes continue to contract and become much shorter and more tightly coiled than at normal metaphase. As the diplo-chromosomes undergo this shortening the divergence between their arms increases (pl. 1, fig. 3). This is probably due to the tightening of the coil rather than to any repulsion between chromosomes.

The division of the SA-region is long delayed but eventually takes place. The two members of a diplo-chromosome now straighten out and frequently lie in parallel arrangement (pl. 1, figs. 5, 6). They may be long or short depending on the time of division; they may be scattered (pl. 1, fig. 5) or may be arranged about an achromatic sphere (pl. 1, fig. 6). The division of the SA-region does not always take place at exactly the same stage of c-mitosis. Rarely chromosomes that are beginning to take on anaphase chromosome characteristics are still in the form of diplo-chromosomes (pl. 1, fig. 7).

Although some spindle substance is probably present in *Allium* during c-mitosis it never becomes organized into an effective spindle. There is no

anaphase movement of chromosomes. They remain in the center of the cell in the tetraploid number and begin the reversion process which results in a 4n restitution nucleus. This process is illustrated in plate 1, figures 7–15. The tightly coiled chromosomes, single or diplo, begin to despiralize and to take on the characteristics of anaphase chromosomes (fig. 7). This condition is followed by further despiralization and the accompanying physical changes normally seen in telophase chromosomes (figs. 8 to 12). A nucular membrane begins to form around the whole group or around smaller groups or isolated chromosomes. In most cases the presence of the achromatic sphere prevents the chromosomes from gathering together in one compact group and results in the strange lobulated forms assumed by early restitution nuclei (figs. 10, 11, 13, 14, 15). The sphere of spindle substance is slow in disappearing and the regions occupied by individual chromosomes are well marked until the restitution nucleus reaches the resting stage (figs. 11, 12).

Apparently not all c-mitoses in *Allium* have an achromatic sphere stage. Scattered diplo-chromosomes and scattered singles are found in cells which give no indication of an achromatic sphere (pl. 1, figs. 3, 5, 16). This difference in the type of c-mitosis may be connected with the mitotic stage of the cell when first subjected to the influence of colchicine.

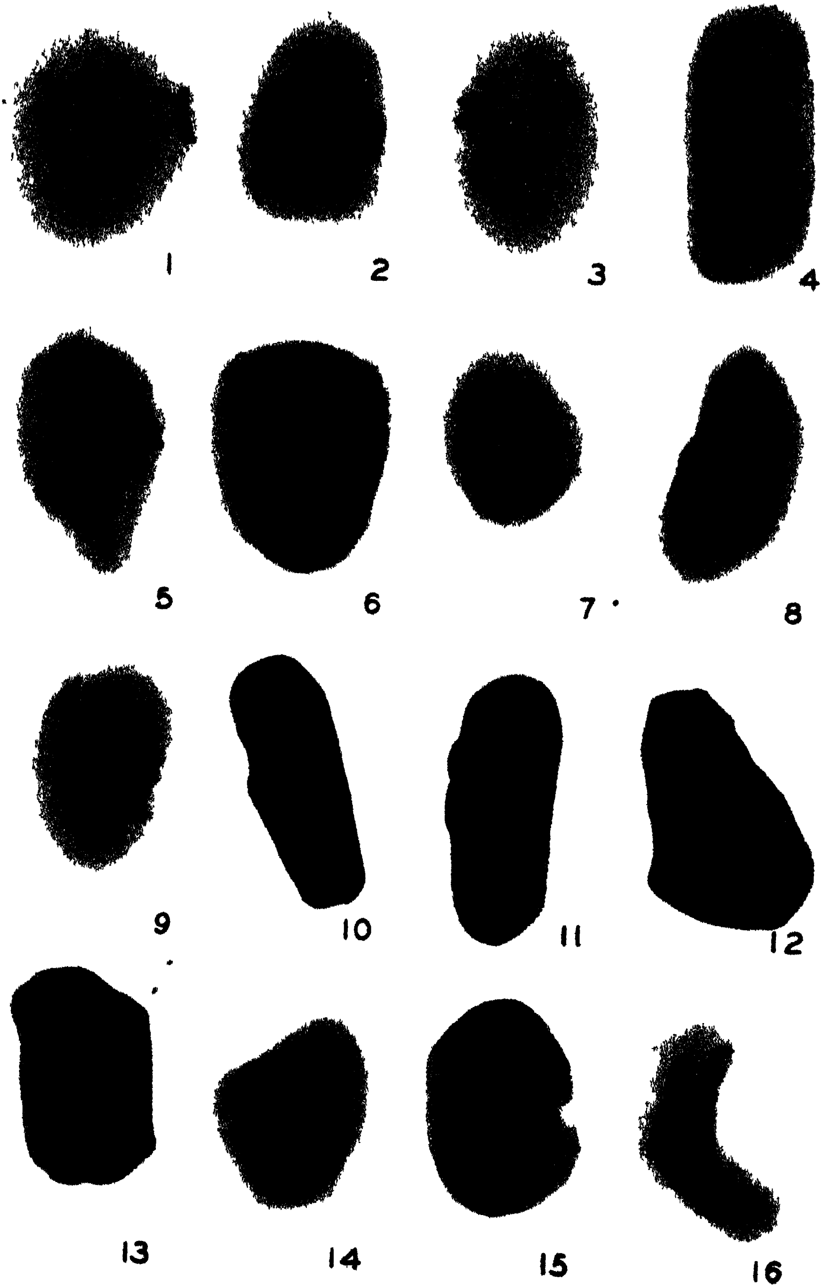
OBSERVATIONS ON SPINACIA

Definition of Terms Covering Special Effects. C-mitosis in *Spinacia* presents some new and some slightly different stages from those described for *Allium* and other material. The first of these differences is the scattered diplo-chromosome stage. The diplo-chromosomes of *Spinacia* are similar in structure to those of *Allium* but differ in arrangement. When first found they are scattered irregularly in the central region of the cell constituting what is here termed the scattered diplo-chromosome stage.

Another stage occurring frequently is the clumped metaphase stage. Here the chromosomes are aggregated to form a dense knot. In a few instances clumps were found consisting of pro-metaphase chromosomes. Most frequently they consist of the diploid number of diplo-chromosomes and less frequently of the tetraploid number of single chromosomes. Cases are found in which one or a few single or diplo-chromosomes lie outside the clump.

Explanation of plate 1

C-mitosis in *Allium cepa*. Magnification of all photomicrographs × 750. FIG. 1. Prometaphase. FIG. 2. Diplo-chromosomes around achromatic sphere. FIG. 3. Scattered diplo-chromosomes. FIG. 4. Diplo-chromosomes around achromatic sphere. FIG. 5. Scattered single chromosomes. FIG. 6. Single chromosomes around achromatic sphere. FIG. 7. Achromatic sphere with diplo-chromosomes in anaphase condition. FIGS. 8–11. Early reversion phase, chromosomes in anaphase and telophase condition around remnant of achromatic sphere. FIG. 12. Reversion nucleus with chromosomes in telophase condition and no evidence of achromatic sphere. FIGS. 13, 14. Early restitution nucleus lobulated in shape. FIG. 15. Restitution nucleus. FIG. 16. C-metaphase and restitution nucleus without achromatic spheres.



BERGER AND WITKUS: SPINACIA OLERACEA

. Other clumps of a looser nature are also found. They are apparently of a higher degree of polyploidy than clumped metaphases. The chromosomes, single or diplo, are not excessively condensed and radiate out from the center like spines. This is called the echinus stage (pl. 2, figs. 38, 39).

Another stage of frequent occurrence in *Spinacia* but lacking in *Allium* and apparently in other material thus far investigated is the prochromosome stage. The term prochromosome is here used not in its current cytological meaning but in a sense similar to that of Wilson (1925) in his description of insect spermatogenesis. It refers to the entire chromosome in a highly condensed state, being shorter and broader than at c-metaphase. A series of prochromosome stages from sectioned material is shown in plate 2, figures 19–23. Similar stages from smeared material are illustrated in figures 30, 31, 32, 33.

The term reversion phase or restitution nucleus formation, is applied to the stage during which the prochromosomes revert to the resting stage condition.

Experimental Results. A 0.25 per cent solution of colchicine was found to be the most suitable concentration for *Spinacia* and was used in most of the experiments. A 0.06 per cent solution brought about similar effects but they were neither as numerous nor as striking. The results recorded here were all obtained after treatment with the 0.25 per cent solution. Root tips of germinating seeds were exposed to this concentration for one, five, and twelve hour periods. The twelve-hour treatment was found to be too long an exposure, causing the death of the root tip.

Results of One-Hour Treatment with 0.25 per cent Colchicine. Material treated for one hour and fixed after one-half hour washing showed very few clumped metaphases, a few scattered diplo-chromosome stages and no prochromosomes. Some normal metaphases, anaphases, and telophases were present in cells that were either at metaphase with a fully formed spindle or at some later mitotic stage when first subjected to colchicine. In material treated for one hour and fixed five hours later the number of clumped metaphases had increased, there were few scattered diplo-chromosome stages, no prochromosomes and no normal divisions. In tips fixed twenty-four hours after treatment a bulbous swelling directly behind the meristematic region was evident. The number of clumped metaphases had greatly increased and there were many scattered diplo-chromosome stages. Prochromosome stages appeared for the first time, indicating the beginning of the reversion phase, and a few normal metaphases and telophases were present, showing that recovery from the influence of colchicine was beginning. Forty-eight hours after treatment the bulbous swelling was less prominent, the clumps, prochromosomes, and scattered diplo-chromosomes had disappeared, and normal

divisions were present. Evidently recovery from one hour treatment begins after twenty-four hours and is complete after forty-eight hours.

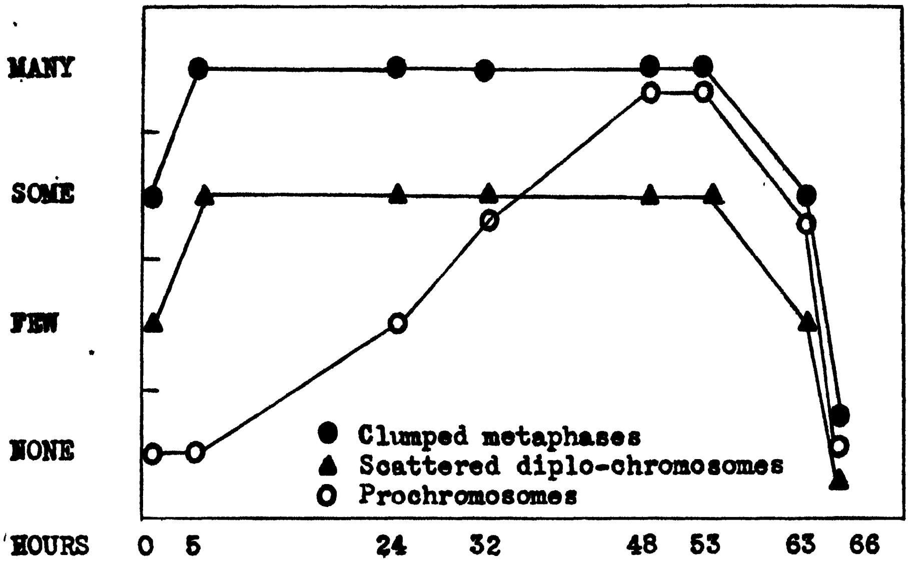
Results of Five-Hour Treatment with 0.25 per cent Colchicine. Root tips treated for five hours and fixed after one-half hour washing showed some clumped metaphases, a few scattered diplo-chromosomes, no prochromosomes and a few prophases. Five hours later there were many clumped metaphases, no prochromosomes, some scattered diplo-chromosomes and no normal divisions. Tips fixed twenty-four hours after exposure again displayed a bulbous swelling just behind the meristematic region. There were many clumped metaphases present, some scattered diplo-chromosomes, a few prochromosome stages but no normal divisions. Forty-eight hours after treatment the swelling was still present and there were many clumped metaphases, some scattered diplo-chromosome stages and many prochromosome stages. There were no normal divisions. Tips fixed fifty-three hours after treatment were very similar to those fixed after forty-eight hours. At sixty-three hours the swelling was smaller and some clumped metaphases were still present. There were a few scattered diplo-chromosomes, some prochromosomes, and a few normal metaphases and anaphases. At sixty-six hours after treatment the swelling had disappeared and there were no clumped metaphases, no scattered diplo-chromosomes, and no prochromosomes. Normal divisions were present. Tips fixed sixty-nine and seventy-two hours after treatment showed similar results.

The experimental results are graphically represented in the accompanying graphs (figs. 17, 18). A comparison of the two graphs shows that one-hour and five-hour treatments brought about similar kinds of cytological effects. After one-hour treatment recovery was complete after forty-eight hours; after five-hour treatment many more cells showed colchicine effects and recovery was not complete until sixty-six hours had elapsed.

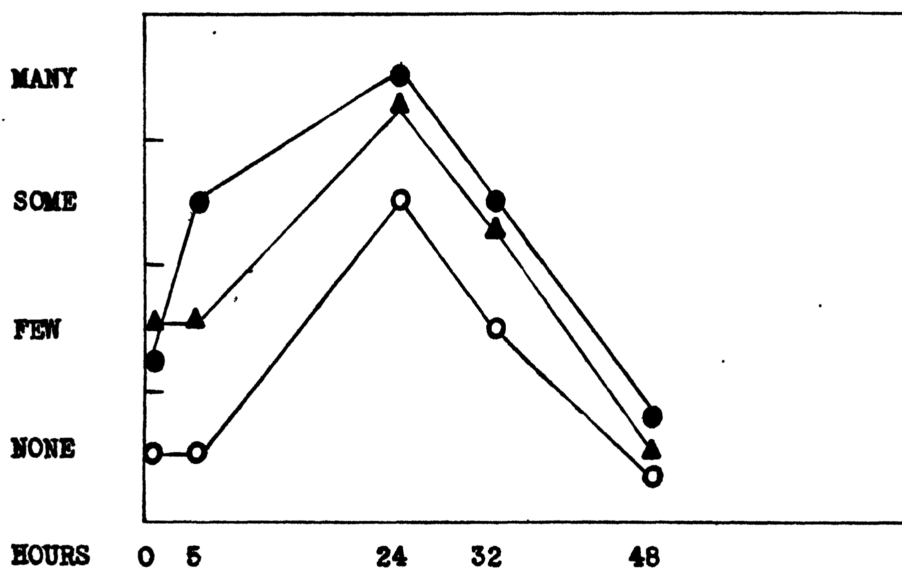
The graphs show that clumped metaphases were always more numerous than the scattered diplo-chromosome stages and hence are probably of longer duration. The scattered diplo-chromosome stage has the same type of curve as the clumped metaphases, they appear and disappear together. The prochromosome stage appeared later than the clumps and the scattered diplo-chromosomes, reached a maximum frequency late in the effective period and disappeared at complete recovery.

It was at first thought that some of the different stages and effects encountered might be located in different regions of the tip. After examining sectioned material, however, it was found that all these stages occurred in all regions of the meristem, plerome, periblem, and dermatogen.

Description of c-Mitosis in Spinacia. In *Spinacia* as in other material under the influence of colchicine the prophases proceed normally. The chromosomes contract attaining their metaphase length at late prometaphase (pl. 2, fig. 24). There is no evidence of any spindle formation and the chro-



17



18

FIG. 17. Frequency of definite effects in *Spinacia* at various time intervals after five-hour treatment with 0.25 per cent colchicine. FIG. 18. Frequency of definite effects in *Spinacia* at various time intervals after one-hour treatment with 0.25 per cent colchicine.

mosomes do not undergo congression on an equatorial plate but remain scattered in the center of the cell in their prometaphase positions. This condition may be considered as the beginning of c-metaphase. This stage in the absence of a spindle is greatly prolonged and, as in *Allium,* the chromosomes undergo marked changes.

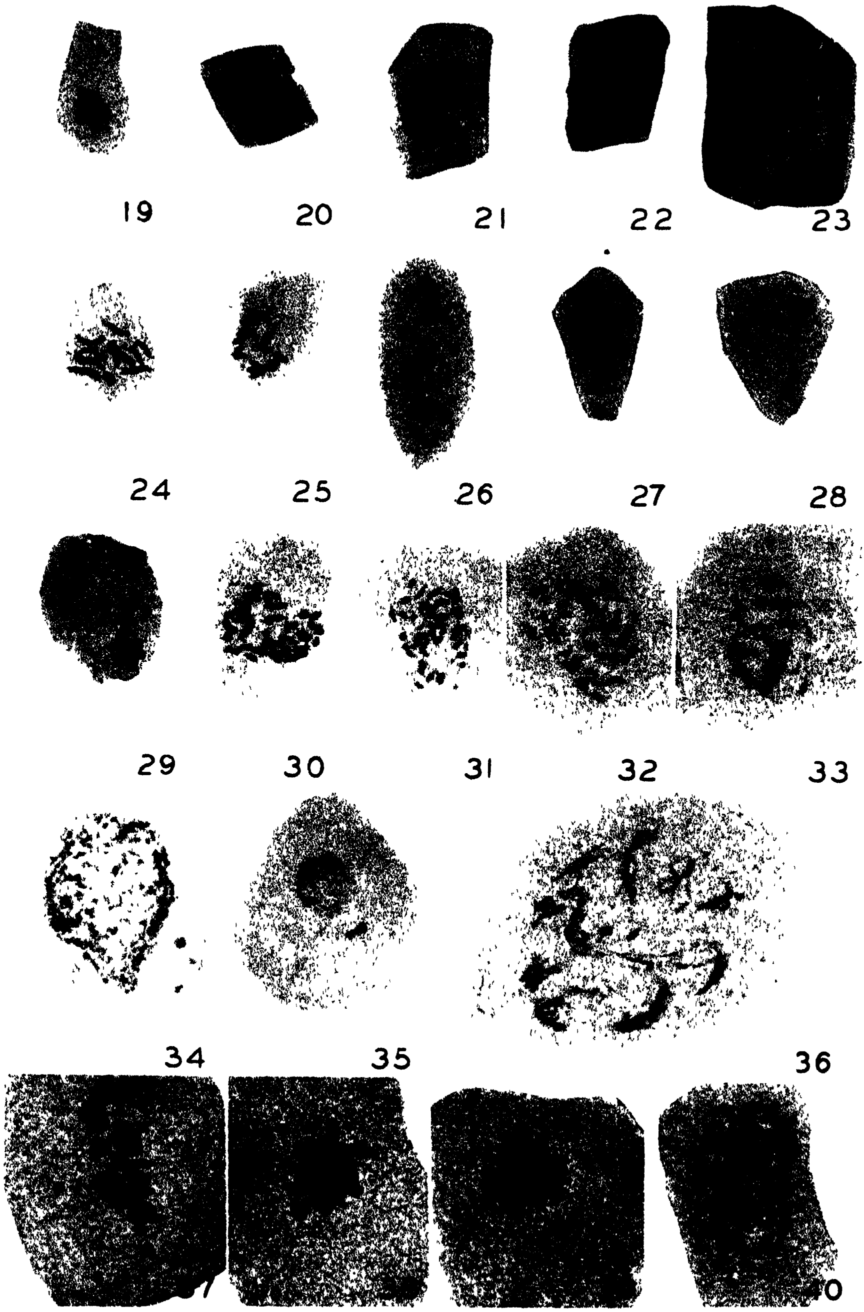
The division of the SA-region is delayed greatly. The long duration of c-metaphase, estimated to range from thirteen to fifty-eight hours, permits a much longer action of the spiralizing forces and the diplo-chromosomes become very tightly coiled and greatly shortened (pl. 2, figs. 25, 26). Homologous arms of the diplochromosomes diverge at their free ends. The divergence is not so pronounced as that found in *Allium* and may be due to the action of repulsion forces or, more probably, to the extreme tightness of the coil.

The scattered diplo-chromosomes eventually come together forming a dense clump (pl. 2, fig. 27). The division of the SA-region usually takes place while the clumping is in progress and partial clumps are found with either diplo-chromosomes (fig. 28) or singles (fig. 29) lying outside the clump. Rarely the division of the SA-region takes place before clumping begins, resulting in cells with scattered singles (fig. 26) in the tetraploid number. The clumped metaphase condition is evidently of long duration, since the number of such clumped metaphases increases with the time under the influence of colchicine. Diplo-chromosomes or singles lying at a distance from the center of the cell are occasionally not included in the clump or in the subsequent restitution nucleus (figs. 28, 29, 35).

In the absence of a spindle neither nuclear division nor cytokinesis ensues and the clumped metaphase stage is followed by a reversion phase which results in a tetraploid restitution nucleus. We have termed the first part of this process the prochromosome stage. The clump loosens up, the single chromosomes separate from one another and are seen to be shorter and thicker with the SA-region no longer discernible (pl. 2, figs. 19–22). At times there are indications of chromatic connecting strands between the chromosomes (figs. 20, 21). A nuclear membrane is formed at this stage. The nucleus en-

Explanation of plate 2

C mitosis in *Spinacia oleracea.* Magnification of all photomicrographs ×750. FIGS. 19–23. Series of prochromosome stages from sectioned material. Figures 24 to 40 are from smear preparations. FIG. 24. Prometaphase. FIG. 25. Scattered diplo-chromosomes. FIG. 26. Scattered singles. FIG. 27. Clumped metaphase. FIG. 28. Clumped metaphase with two scattered diplo-chromosomes. FIG. 29. Clumped metaphase with a few scattered singles. FIGS. 30–33. Successive prochromosome stages. FIG. 34. Reversion phase following prochromosome stage. FIG. 35. Restitution nucleus with one diplo-chromosome in the cytoplasm. FIG. 36. Secondary pairing in prophase of an octoploid cell. FIG. 37. Secondary pairing at early c-metaphase of an octoploid cell. FIG. 38. Echinus stage with diplo-chromosomes. FIG. 39. Echinus stage with single chromosomes. FIG. 40. Prochromosome stage in an octoploid cell.



BERGER AND WITKUS: SPINACIA OLERACEA

larges and the chromosomes become evenly spaced about the periphery (figs. 22, 23), the general appearance being similar to that of the preleptotene prochromosome stage described in insect spermatogenesis (Wilson 1925).

As the prochromosomes become more widely spaced they begin to despiralize and the SA-region again becomes evident. This despiralization is apparently twofold, consisting of a slight separation of the gyres in the central region of the chromosome and a much more marked relaxation of the coil at the ends accompanied by a loss of chromaticity (pl. 2, figs 30–33). This terminal relaxation of the coil (fig. 33) progressively involves a greater part of the chromosome while the prochromosomal or more condensed region becomes smaller and eventually disappears. At the end of the prochromosome stage the chromosomes are in the form of thin threads in a uniform relic spiral (fig. 34). The remainder of the reversion process consists of further despiralization, attenuation of the chromonemata, and loss of chromaticity. In this way a tetraploid resting nucleus is formed.

When a tetraploid cell enters prophase the twenty-four chromosomes are associated in twelve pairs. This primary pairing is probably an indirect effect of colchicine treatment being due to the lack of anaphase separation in the previous c-mitosis.

Octoploid cells were found which showed the forty-eight chromosomes associated in twelve groups of four chromosomes each. This secondary pairing is seen at prophase (pl. 2, fig. 36) and at early c-metaphase (fig. 37) before the scattered chromosomes undergo clumping. Such cells were normal polysomatic paired tetraploids which underwent one c-mitosis, becoming secondarily paired octoploids. Similar secondarily paired octoploids could presumably have arisen from diploid cells by two successive c-mitoses. In the present case this possibility is eliminated by the experimental data (figs. 17, 18) which shows that only one complete c-mitotic cycle occurred in these experiments, although some prophases of a second c-mitosis were found.

The clumped metaphases of polyploid cells are looser than the diploid clumps and the chromosomes, single or diplo, radiate out like spines (pl. 2, figs. 38, 39). This is the echinus stage. The prochromosome stage (fig. 40) and later reversion stages in polyploids are similar in structure to those of diploid cells.

DISCUSSION

The most significant difference between c-mitosis in *Allium* and in *Spinacia* is the presence of an achromatic sphere in the former and its total absence in the latter. Shimamura (1939) is probably correct in his view that the achromatic sphere is formed of spindle substance which is not organized into an effective spindle. Apparently the protoplasm of *Spinacia* is of such a nature that it is unable to form any spindle substance in the presence of colchicine, while the protoplasm of *Allium* does elaborate some of the mate-

rial necessary for spindle formation. In the absence of the achromatic sphere the chromosomes of *Spinacia* form dense clumps at a stage wherein the diplo-chromosomes of *Allium* are gathered around the sphere.

The many strange forms assumed by restitution nuclei in *Allium* are due to the persistent presence of the sphere, which continues well into the reversion phase and hinders the association of the chromosomes in a common restitution nucleus. Multinucleate cells, forms with macro and micronuclei, and lobulated nuclei are all due to the persistence of the achromatic sphere. In *Spinacia* no such unusual forms are encountered, the restitution nucleus regularly being spherical or nearly so.

Another striking difference between *Spinacia* and *Allium* is the presence of the prochromosome stage in *Spinacia* and its complete absence in *Allium*. We can offer no suggestion as to the cause or significance of this difference. That it is a colchicine effect is clear since there is nothing resembling this stage in untreated material.

SUMMARY

1. In *Allium* under the influence of colchicine some unorganized spindle substance is produced and takes the form of an achromatic sphere about which the diplo-chromosomes gather at c-metaphase.

2. In *Spinacia* no achromatic sphere of spindle substance is formed and the diplo-chromosomes form dense clumps at c-metaphase.

3. The many strange shapes of restitution nuclei in *Allium* are due to the presence of the achromatic sphere.

4. Restitution nuclei in *Spinacia* are regularly spherical or nearly so.

5. The chromosomes of *Allium* during the reversion phase pass through structural conditions similar to those of normal anaphase and telophase chromosomes.

6. The chromosomes of *Spinacia* during the reversion phase do not resemble anaphase or telophase chromosomes but go through a stage similar to the prochromosome stage of insect spermatogenesis.

BIOLOGICAL LABORATORY, FORDHAM UNIVERSITY
NEW YORK

Literature Cited

Beams, H. W. & King, R. T. 1938. An experimental study of mitosis in somatic cells of wheat. Biol. Bull. **75**: 189–207.

Levan, Albert. 1938. The effect of colchicine on root mitoses in *Allium*. Hereditas **24**: 471–486.

Shimamura, T. 1939. Cytological studies of polyploidy induced by colchicine. Cytologia **9**: 486–494.

Walker, R. I. 1938. The effect of colchicine on somatic cells of *Tradescantia paludosa*. Jour. Arnold Arb. **19**: 158–162.

Wilson, E. B. 1925. The cell in development and heredity.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 5, pp. 467–472 SEPTEMBER, 1943

MORPHOLOGICAL VARIATION AND CYTOLOGY OF BROMUS INERMIS[1]

IRVING WILLIAM KNOBLOCH[2]

Bromus inermis Leyss., smooth brome grass, was introduced into this country from Eurasia about 1882. The species is a long-lived perennial which spreads rapidly by rhizomes, and is a valuable grassland and forage crop for the prairie and plains states from Canada to Kansas. Brome grass survives under adverse soil conditions and is more drought-resistant than some more commonly used grass species.

Variation has been noted in this species by several investigators. Zherebina (1931, 1933), Waldron (1921), Keyser (1913), and Frolik and Newell (1941) noted that *Bromus inermis* varies considerably in height, bushiness, seed production, yield of hay, length and width of blade, protein content, rhizome development, heat and drought tolerance, and disease resistance. The present study of variation emphasizes, for the most part, characters not studied by previous investigators. In compiling the known ranges of measurements for eleven characters in *Bromus inermis*, as shown in table 1, many authors were consulted, but no higher or lower limits for the characters were found than those provided by Hegi (1906), Hitchcock (1914, 1935), Shear (1900), Waldron (1921), Stebler and Schröter (1889), Armstrong (1937), Beal (1896), and Nowosad, Swales, and Dore (1936).

The cytology of smooth brome grass has also been investigated. Avdulov (1928, 1931) reported the diploid number to be 56. Stählin (1929) recorded the diploid number as 42. Nielsen (1939) confirmed Avdulov's count and added a 70-chromosome race.

The present study emphasizes the range of morphological variation existing in the species. The chromosome counts on numbered strains and selections will facilitate breeding work and the ultimate production of desirable types for local conditions.

MATERIALS AND METHODS

The plants used in the present study were obtained from the forage crops breeding nursery of the Iowa Agricultural Experiment Station, Ames,

[1] Portion of a dissertation submitted to the Graduate Faculty of Iowa State College in partial fulfillment for the degree of Doctor of Philosophy.

[2] The writer wishes to express his appreciation to Dr. J. E. Sass for suggesting the problem, and for helpful encouragement and advice throughout the course of the investigation and during the preparation of the manuscript. Thanks are also due to Dr. G. J. Goodman and Dr. I. J. Johnson for advice and to Dr. C. P. Wilsie for the use of the brome grass plants in the forage crops nursery of the Iowa Agricultural Experiment Station.

Iowa. These plants had been established from open-pollinated single plant selections from many sources. Measurements made on plants from sixteen different strains and selections were compared with the published range of measurements. In the cytological investigations, plants belonging to fifteen different strains and selections were used. Both root tips and pollen mother cells were examined. Variations of the Nawaschin (Craf) formula, FAA, and Carnoy's fluid were used, and a crystal violet–iodine staining technique was followed.

MORPHOLOGICAL VARIATION

The characters selected for a study of variation are given in table 1, which shows the previously known range, the ranges encountered locally,

TABLE 1. *Range in measurements of various characters in Bromus inermis by eight authors compared to measurements of plants grown at Ames, Iowa.*

	Culm (mm.)	Sheath	Blade (mm.)	Ligule (mm.)	Panicle (mm.)	Spikelet (mm.)	First glume (mm.)	Second glume (mm.)	Lemma (mm.)	Palea (mm.)	Floret No.
Various authors	300–1400	Glabrous or pubescent	5–19 wide 100–400 long	0.5–2	100–203.2	20–27	4–5	6–8	7–14	Equaling lemma	2–10
Local measurements	480–1080	Glabrous or pubescent	3.5–9 wide 130–300 long	1–2	80–200	10–30	3–7	4–9	7–13	5–10	3–10
Total range	300–1400	Glabrous or pubescent	3.5–19 wide 100–400 long	0.5–2	80–203.2	10–30	3–7	4–9	7–14	5–14	2–10

and the total range now known to exist. Certain characters have been omitted from the table because no marked variation was noted. For example, the rhizomes are always creeping, the rachillas and secondary branches are always pubescent, the paleas are 2-nerved, the lemmas are 5–7-nerved, the first glumes are generally one-nerved, the second glumes are always 3-nerved, the ligules are always lacerate, and the culms are generally glabrous except for nodal hairs.

The following characters on local plants fall within the published ranges: culm length, presence or absence of hairs on the sheath, length of blade, length of ligule, length of lemma, and number of florets per spikelet. The following characters were found to be above or below the published

range: width of blade, height of panicle, length of spikelet, length of first glume, length of second glume, and length of palea. Table 1 shows, therefore, that *Bromus inermis* varies considerably in the eleven selected characters. Wide variation was also found to occur within particular strains or selections.

MITOSIS

Mitosis is observed most easily in the root-tips. In addition to the nuclear reticulum, each prophase nucleus contains 1–5 usually spherical nucleoli varying from 1.4 to 6.8 microns in diameter. Somatic chromosomes at metaphase are predominantly J- or V-shaped (fig. 1), with sub-median or median spindle-fiber attachments. Chromosomes vary in length from 4.4 to 6.8 microns and are approximately 0.6 microns in thickness.

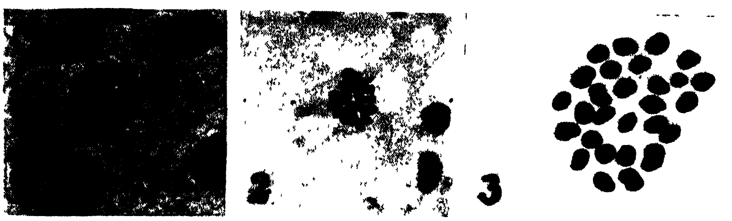


FIG. 1. Mitotic metaphase in a root tip cell of a hexaploid plant ($2n = 42$). $\times$ 800. FIG. 2. Metaphase of first division in a pollen mother cell of a hexaploid. $\times$ 800. FIG. 3. Metaphase of the first division in a pollen mother cell of an octoploid ($2n = 56$). $\times$ 1,500.

Mitosis appears to be rather regular in the root-tips of smooth brome grass. Precise metaphase alignment of the spindle-fiber attachments occurs. No evidence of lagging or other irregularity was noted.

MEIOSIS

The pollen mother cells are favorable for studies of some aspects of meiosis. Early prophase studies were not emphasized. Late prophase chromosomes are all straight rods, and during diakinesis they range in length from 2.6 to 5.2 microns. One nucleolus is present in prophase and persists up to late diakinesis. Usually all the pollen mother cells of a field exhibit the same stage of meiosis, but occasionally both metaphase and anaphase or even metaphase and telophase figures are found together.

At metaphase the chromosomes range from 1.3 to 2.6 microns in length. Usually the metaphase plates exhibit only bivalents, but occasionally both bivalents and univalents are found on the same plate.

During anaphase, marked irregularity is evident. In some cells a few chromosomes reach the polar region well in advance of the majority. More frequently, a few chromosomes lag and reach the poles late. Some bivalents

evidently fail to disjoin as quickly as others do. An unusual case was noted in which 28 bivalents, the normal number for that plant, separated into two groups of 14 bivalents each, which moved to opposite poles as bivalents.

Many of the laggards arrive at the poles in time to be included in the telophase nuclei. Frequently, however, one or more chromosomes may be observed lying in the cytoplasm near the reorganized nuclei. These chromosomes probably disintegrate, for they are not often seen in the diads. Occasionally, chromosomes become enmeshed in the partition wall of the diad.

The second division follows the first division quickly. The spindle is oriented at right angles to the spindle of the first division and in the same plane, resulting in the four microspores lying in one plane. In general, the second division exhibits regularity, but precocious as well as lagging anaphase separation may be observed. The four microspores frequently show chromatin material in the cytoplasm left from either the first or second divisions or both.

An examination of 27 plants belonging to 15 strains and selections showed that five of the plants have a diploid number of 56 (fig. 3), and 22 plants have a diploid number of 42 (fig. 2).

In view of the fact that *Bromus inermis* varies greatly morphologically and that cross-pollination freely occurs, it is possible that natural crossing is responsible for some of the known chromosome irregularities. These irregularities may furnish a basis for the morphological variation in the species. It is also probable that the environment exerts an influence upon the expression of the characters.

DISCUSSION

The present study of variation in smooth brome grass reveals a greater variation in six characters than hitherto reported. In showing extensive variation in morphological characters, smooth brome grass is similar to other grass species. For example, Wilkins (1928) noted variation in *Anthoxanthum* and *Triticum;* H. Witte (1912) found plants of *Phleum pratense, Dactylis glomerata, Festuca pratensis,* and *Avena elatior* to vary greatly within the species; Webber (1912), Hayes and Barker (1922), and Clark (1910) studied variation in *Phleum pratense* particularly; Gregor and Sansome (1927) executed variation studies on *Phleum, Lolium,* and *Dactylis;* and Brown (1939, 1941) noted that plants of *Poa pratensis* vary considerably.

Müntzing (1936) estimated that at least 100 species of plants are known to have intraspecific races differing in chromosome number. Such races also show morphological variation. Many grasses are included in Müntzing's list such as *Phleum pratense, P. alpina, Aegilops triaristata, A. crassa, Festuca ovina, F. pratense, Tripsacum dactyloides,* and *Dactylis glomerata.*

Fults (1942) found six biotypes in *Bouteloua gracilis.* Rancken (1934) noted that *Festuca pratensis, Poa pratensis,* and *Alopecurus pratensis* vary among themselves.

In the present study, five of the twenty-seven plants are octoploids and twenty-two plants are hexaploids. Avdulov's and Nielsen's chromosome counts of 56 and Stählin's count of 42 are all confirmed. No race with 70 chromosomes was found such as Nielsen reported.

SUMMARY

Measurements on eleven morphological characters in *Bromus inermis* revealed six characters which vary to a greater extent than previously reported. These six characters are: blade width, length of panicle, length of spikelet, length of first glume, length of second glume, and length of palea.

Mitosis in the root tips is regular. The somatic chromosomes range in length from 4.4 to 6.8 microns and are approximately 0.6 microns in diameter. Metaphase meiotic chromosomes range from 1.3 to 2.6 microns in length. Precocious disjunction and lagging were observed in the first and second divisions.

Twenty-seven plants belonging to fifteen strains and selections were examined for chromosome number. Five of the plants have a diploid number of 56, and 22 plants have a diploid number of 42 chromosomes.

Natural crossing between the highly variable strains and selections is believed to account for at least some of the chromosome irregularity exhibited by the species. Meiotic irregularities in the pollen mother cells possibly account for some of the morphological variation shown. The environment may affect the expression of characters.

Department of Botany, Iowa State College
Ames, Iowa

Literature Cited

Armstrong, S. F. 1937. British grasses and their employment in agriculture. Cambridge Univ. Press.

Avdulov, N. P. 1928. Karyo-systematische Untersuchung der Familie Gramineen. Allruss. Bot. Kong. Ber. **1928:** 65–66. [Not seen; cited in U. S. Dept. Agr. Yearbk. 1937, p. 1099.]

————. 1931. Karyo-systematische Untersuchung der Familie Gramineen. Trudy Po Prikl. Bot. Genet. Selek. Prilozh. (Bull. Appl. Bot. Genet. Plant Breeding Suppl. 44): 353–448.

Beal, W. J. 1896. Grasses of North America. 2 Vol. New York.

Brown, W. L. 1939. Chromosome complements of five species of *Poa* with an analysis of variation in *Poa pratensis.* Am. Jour. Bot. **26:** 717–723.

————. 1941. The cytogenetics of *Poa pratensis.* Ann. Mo. Bot. Gard. **28:** 493–516.

Clark, C. F. 1910. Variation and correlation in timothy. New York (Ithaca) Exp. Sta. Bull. 279.

Frolik, A. L. & Newell, L. C. 1941. Bromegrass production in Nebraska. Univ. Nebr. Coll. Agr. Exp. Sta. Circ. 68.

Fults, J. L. 1942. Somatic chromosome complements in *Bouteloua*. Am. Jour. Bot. **29**: 45–55.

Gregor, J. W. & Sansome, F. W. 1927. Experiments on the genetics of wild populations. Jour. Gen. **17**: 349–364.

Hayes, H. K. & Barker, H. D. 1922. The effects of self-fertilization in timothy. Jour. Am. Soc. Agron. **14**: 289–293.

Hegi, G. 1906. Illustrierte Flora von Mittel-Europa. München.

Hitchcock, A. S. 1914. A textbook of grasses. New York.

————. 1935. Manual of the grasses of the United States. U. S. Dept. Agr. Mics. Publ. 200.

Keyser, A. 1913. Variation studies in brome grass (A Preliminary Report). Colo. Exp. Sta. Bull. 190.

Müntzing, A. 1936. The evolutionary significance of autopolyploidy. Hereditas **21**: 263–378.

Nielsen, E. L. 1939. Grass studies III. Additional somatic chromosome complements. Am. Jour. Bot. **26**: 366–372.

Nowosad, F. S., Swales, D. E. N. & Dore, W. G. 1936. The identification of certain native and naturalized hay and pasture grasses by their vegetative characters. Pasture Studies IX. Tech. Bull. 16, MacDonald Coll., McGill Univ.

Rancken, G. 1934. Cytological studies of valuable meadow grasses with special reference to structural irregularities in the chromosome complements. Suom. Maataloustiet. Seura, Julkaisu. Acta Agralia Fennica **29**: 1–96. [Transl. Title Ger. Not seen, abstracted in A. J. Pieters, *A Digest of Some World Pasture Research Literature Exclusive of the Continental United States and Canada.* U. S. Dept. Agr. Bur. Pl. Ind. 1937.]

Shear, C. L. 1900. A revision of the North American species of *Bromus* occurring north of Mexico. U. S. Dept. Agr. Div. Agros. Bull. 23.

Stählin, A. 1929. Morphologische und Zytologische Untersuchungen an Gramineen. Wiss. Arch. Landw. **1**: 330–398.

Stebler, F. G. & Schröter, C. 1889. The best forage plants. (Transl. by A. N. McAlpine.) London.

Waldron, L. R. 1921. Some physical and chemical studies of certain clones and sibs of brome grass. N. Dak. Agr. Sta. Bull. 152 (Res. Bull. 1).

Webber, H. J. 1912. The production of new and improved varieties of timothy. N. Y. (Cornell) Exp. Sta. Bull. 313.

Wilkins, V. E. 1928. Anatomical studies of certain gramineae. Ann. Bot. **42**: 305–316.

Witte, H. 1912. Multiplicity of forms in the most important forage grasses. Sveriges Utsädesför. Tidskr. **22**: 65–118.

Zherebina, Z. N. 1931. Essay of a botanical agronomical study of awnless brome grass (*Bromus inermis* Leyss.). Trudy Po Prikl. Bot. Genet. Selek. (Bull. Appl. Bot. Genet. Plant-Breeding) **25**: 201–352.

————. 1933. *Bromus inermis* Leyss. Rastenievodstvo U.S.S.R. **1**: 507–518.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 5, pp. 473–480 SEPTEMBER, 1943

PLANT SUCCESSION ON TALUS SLOPES IN NORTHERN IDAHO AS INFLUENCED BY SLOPE EXPOSURE[1]

R. F. DAUBENMIRE AND A. W. SLIPP

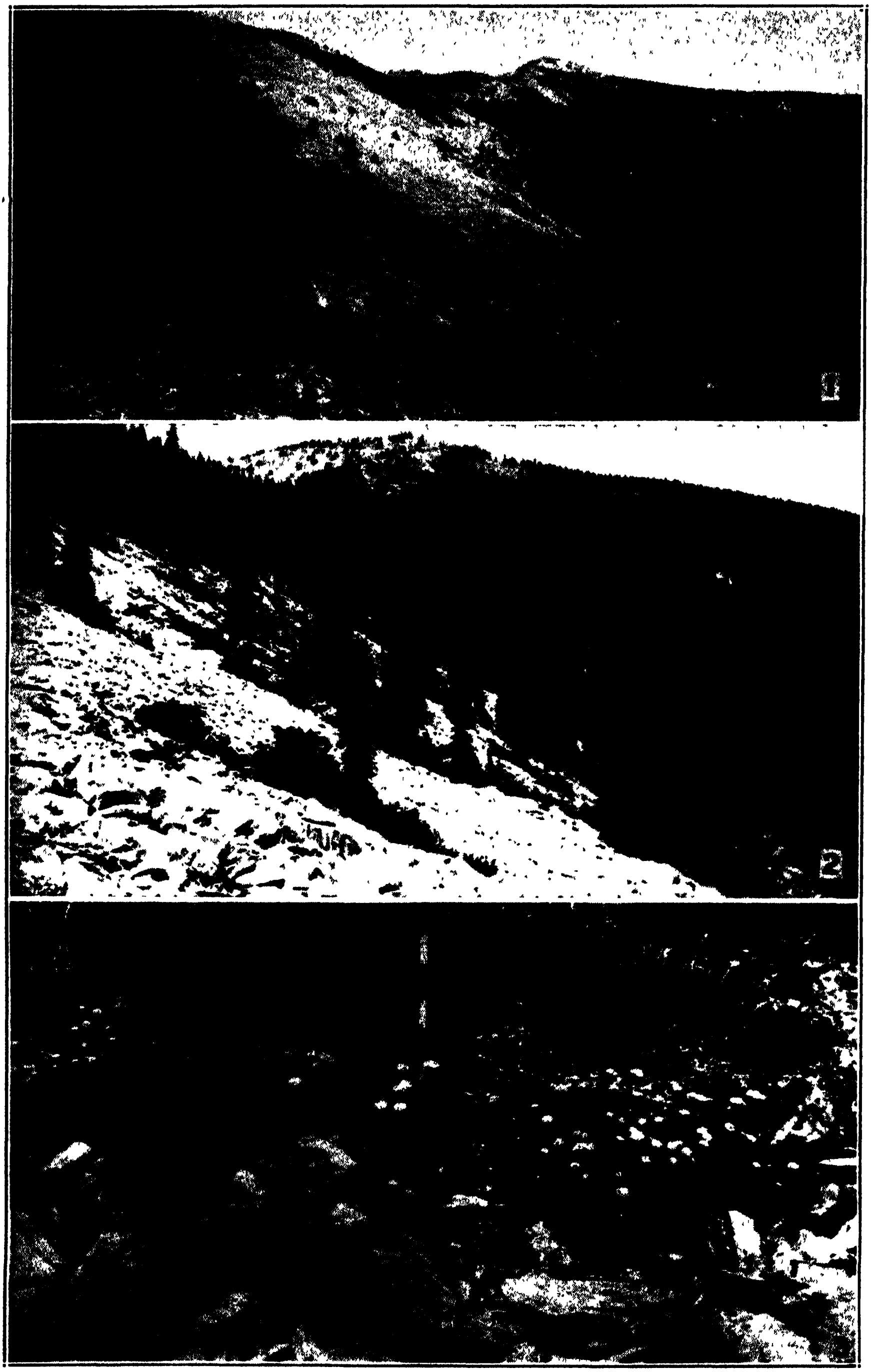
One of the most conspicuous features of the forested regions of northern Idaho is the small treeless areas which occupy portions of the southerly exposures of especially prominent peaks and ridges. These areas, sometimes referred to as parks or balds, begin at the summits of the prominences and extend down over the south-facing slopes sometimes as much as approximately 200 m. Each park is essentially an island of prairie-like vegetation surrounded by belts of shrubs and scattered trees, and then by dense forest. Few if any of the mountains of northern Idaho are high enough to have a climatically determined upper timberline, so these parks are not to be confused with alpine vegetation.

On an east-west ridge in Bonner County, Idaho, approximately midway between Priest and Pend Oreille lakes, the writers were attracted by a series of open talus areas on the north slope where the climax vegetation is forest, and to one which is located on exactly the opposite slope in a park (fig. 1). These talus areas seemed to offer an exceptionally good opportunity to compare the effects of conditions associated with slope exposure upon the course of vegetational development on bare areas otherwise identical. Talus slopes are abundant in the northern Rocky Mountains, but observations were confined to the opposite sides of this single ridge in order to eliminate variations in macroclimate between bare areas. The two rock slides studied are exactly opposite, about 300 meters down the slope on either side of the crest of the ridge.

The talus on both exposures consists of blocks of metamorphosed granite which for the most part vary between one-quarter of a meter and one meter

[1] The writers are indebted to the Northern Rocky Mountain Forest and Range Experiment Station for the use of laboratory and other facilities of the Priest River Experimental Forest which were of material assistance in making this study.

FIG. 1. General view looking east along Looking Glass Ridge. The rock slides studied are in the distance just below the highest knob on the horizon but not visible in this photograph. Just within the forest toward the top left corner of the picture is an area where the topography favors such a heavy accumulation of snow that the trees are extremely dwarfed and misshapen. FIG. 2. General view of fir forest on the north side of Looking Glass Ridge. Note upper edge of park on opposite (south-facing) slope in distance. Elongate strips of vegetation on talus in foreground consist chiefly of *Menziesia ferruginea* and *Abies lasiocarpa*. FIG. 3. Edge of talus on south-facing slope showing mats of *Eriogonum subalpinum* invading the rock mass and preparing the way for grasses. The stake is marked off in decimeters.



in diameter. Among these angular boulders there is practically no finer detritus to serve as soil material. This lack of soil and the instability of the surface layers of rocks are the two major factors which have long retarded the colonization of these areas by plants.

SUCCESSION ON THE NORTH SLOPE

Succession is initiated on the north slope by mosses which become established in the niches formed by the accidental arrangement of boulders. Around the periphery of the open expanse of talus, where nearby trees can exert a sheltering influence, the mosses are very aggressive in that they seem not to demand a better substratum than is provided by the bare rock surface, and the colonies soon spread so as to completely cover the walls of the niches. Toward the central part of the open talus area mosses seem more dependent upon a previous accumulation of weathered rock fragments or bits of litter blown from the forest, and the colonies do not spread so vigorously as near the edge of the forest. The advent of vascular plants, and therefore the continuation of the sere, seems in every case to be dependent upon these moss colonies which provide lodging for the disseminules and hold sufficient moisture to supply the seedlings until their roots have extended down through the cool moist cavities among the talus blocks to the more permanent moisture supplies which lie below.

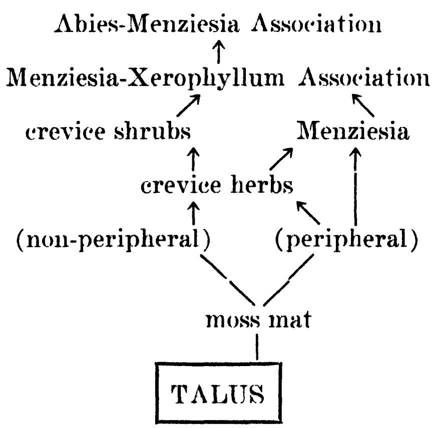
The pioneer vascular plants which enter upon the mosses likewise reflect a slight differentiation between the central and peripheral portions of the talus habitat. Usually herbs such as *Cheilanthes gracillima* D. C. Eaton, *Cryptogramma acrostichoides* R. Br., *Aquilegia flavescens* S. Wats., *Angelica sp.*, *Penstemon fruticosus* (Pursh) Greene, and *Arnica sp.* follow the mosses, but in peripheral regions the shrub *Menziesia ferruginea* Smith may enter the sere at this point. Over most of the talus a wider variety of shrubs including *Ribes viscosissimum* Pursh, *R. lacustre* (Pers.) Poir., *Sorbus occidentalis* (S. Wats.) Greene, *Sambucus melanocarpa* A. Gray, *Rubus*, and *Amelanchier* follows the establishment of the herbs. Thus far there is hardly enough interrelationship between the individuals representing a given stage in succession to refer to each stage as an association. However, the next clearly marked stage of development is a closed association dominated by *Menziesia ferruginea* Sm. and *Xerophyllum tenax* (Pursh) Nutt. The slight difference in successional trend between peripheral and central parts of the talus slope practically disappears with the development of the *Menziesia-Xerophyllum* thicket.

The climax dominant, *Abies lasiocarpa* (Hook.) Nutt., germinates in the shelter of the *Menziesia-Xerophyllum* association, and the final adjustments leading toward stability come about as the trees increase in size and abundance so that a closed forest is formed. *Menziesia* and *Xerophyllum,* which

are the dominants of the preclimax association, persist as the most important plants in the dense undergrowth of the forest. Stability is finally attained by the replacement of relic herbs and shrubs of the open talus by minor constituents of the climax forest.

In general, the initiation of succession upon this north slope is nearly independent of talus activity, but the continuance of succession at a given point of origin depends upon comparative stability which may be provided by either topographic or substratal features. Rolling fragments tend to converge into valley-like depressions down which boulders roll frequently, leaving alternating strips of relatively stable material. Also, less extensive but more permanently stabilized areas may be provided in the lee of exceptionally large boulders which are too deeply imbedded in the detritus to be affected by surface movement. Small rocks are diverted to each side of these larger boulders leaving quiescent areas on the slope immediately below. The island-like thickets which develop at such places always expand most rapidly in a direction at right angles to the contour lines, down the strips of quiescent material which alternate with paths along which the movement of boulders is active. The forest stage makes its first appearance as a narrow strip extending down the axis of these elongate islands of shrubby vegetation (fig. 2).

The sere on the north slope, as described above, may be expressed in a simplified diagram which shows the chief stages as follows:



SUCCESSION ON THE SOUTH SLOPE

The surface of the talus area on the south side of the ridge is not so steep as that on the north slope, so that instability is here not so important a factor in retarding plant invasion. However, the lack of a substratum with adequate water-holding powers appears to be so much more important on this slope that despite the greater stability of the surface, plant invasion of the talus here is at least as slow as on the north slope.

Moss patches, which on the north slope fostered the development of islands of vegetation at scattered loci over the talus surface, are almost entirely lacking on the dry south slope and invasion is accomplished by the marginal encroachment of vascular plants unpreceded by cryptogams. The crustose lichens, which are fairly abundant on the rocks here, seem to be wholly inconsequential in the establishment of higher vegetation.

Eriogonum subalpinum Greene is the most characteristic species leading the mass encroachment of vegetation onto the loose rocks (fig. 3). The dense mat of low stems and leaves produced by this plant is admirably suited for the accumulation of litter and wind-borne mineral fragments. The fringe of *Eriogonum* about the open talus is thin and frequently discontinuous, and in places dead, wind-eroded *Eriogonum* mats demonstrate that plant succession on this slope is vulnerable to reverses during seasons of exceptional drought.

Immediately behind the *Eriogonum* fringe occur the species which compose the prairie-like climax. As stated previously, the permanent plant cover on the most exposed portions of the park is a grassland, while on less exposed situations occur individual trees or small groves of *Pinus albicaulis* Engelm., *Pseudotsuga taxifolia* (Poir.) Brit., and occasionally *Abies lasiocarpa* (fig. 1). There is no evidence whatever that the trees can increase to replace these grasslands under the existing climatic conditions. Among the most conspicuous vascular plants of the grasslands are: *Festuca idahoensis* Elmer, *Agropyron spicatum* (Pursh) Scribn. & Smith,[2] *Xerophyllum tenax* (Pursh) Nutt., *Carex geyeri* Boott., *Arenaria formosa* Fischer, *Lupinus sp.*, *Achillea lanulosa* Nutt., *Aster stenomeres* Gray., *Senecio integerrimus* Nutt., *Hieracium albertinum* Farr. The relatively simple succession on the south slope may be diagrammed as follows:

Forest Association
↑
(less exposed sites)
¦
Festuca–Agropyron Association
↑
Eriogonum
|
$\boxed{\text{TALUS}}$

ENVIRONMENTAL DIFFERENCES ON THE TWO SLOPES

In spite of the short distance separating the two talus areas described above, there is an extremely sharp difference in the seres and the climaxes

[2] In this particular park most plants are of the awnless form, although a few individuals possess short awns.

in which they culminate. Even the floras are almost wholly distinct—the only species in common is *Xerophyllum tenax*. These facts must be interpreted as indicating the existence of some factor or factor-complex which produces a net environmental difference proportionally as great as the vegetational difference.

Frequently the obvious difference in water balance associated with north and south slopes has been attributed to insolation which causes higher transpiration, evaporation, and temperature on the south slope, with the result that both the soil and air are drier there. To determine the extent to which this explanation might be applicable to the ridge studied, comparative measurements of evaporation stress were made. Stations were established in open talus areas on both slopes, as well as in the climax forest on the north slope and the climax grassland on the south slope. The data obtained (table 1)

TABLE 1. *Mean daily water-loss in milliliters from standardized spherical atmometers operated during a 4-week period: June 29–July 27, 1941.*

Location of instruments	North slope	South slope
Open talus		
Large area	41.0	
Small area	29.8	40.5
Climax vegetation	11.2	36.1

show that (a) the evaporation rate is consistently lower in the climax communities than on the primary bare areas, (b) the severity of this factor decreases less as a result of succession on the south than on the north slope, and (c) the evaporation rate alone is not a critical factor governing plant succession here, for the evaporation rate on large talus areas on the north slope may be greater than the rate on a small area on the south slope. The type of vegetational development is correlated with direction of exposure rather than with the size of the talus area; the successional pattern is essentially identical on large and small talus areas on either slope, regardless of differences in evaporation stress.

Other environmental measurements directly applicable to the present problem have been made on both north and south slopes near the west end of the ridge by Hayes.[3] He maintained stations in open situations on both slopes during the summer months for a period of three years. His data show that although summer precipitation and mean daily relative humidity (at 4.5 feet above the ground) are approximately equal on both slopes, wind velocity on the south slope averages 1.1 m.p.h. greater than on the north, and the 3-year average of median maximum duff surface temperatures was 148° F. on the south slope in contrast to 111° on the north slope.

[3] **Hayes, G. C.** 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. U.S.D.A. Circ. 591: 1–39.

The possible importance of lethal soil surface temperatures in the present problem can be discounted at once, because species characteristic of the north slope cannot grow even in the shade cast by the dense tall grasses which cover the south exposure.

Although measurements of wind and of duff moisture both indicate a less favorable water balance on the south exposure, even their cumulative influence is not commensurate with the great difference in vegetation on the two slopes. Clearly none of the atmospheric conditions measured by Hayes or by the writers differs sufficiently in midsummer to account for the vast difference in xerism which is indicated by the vegetation itself.

Two aspects of winter climate seem to deserve consideration with regard to this problem of environmental differentiation. There is abundant evidence in the Rockies that at upper timberline strong winter winds may evaporate more water from trees than can be absorbed from the cold soil so that winter killing results. This form of injury invariably results in strikingly asymmetrical trees, and since the pines and Douglas firs around the open grassland on Looking Glass Ridge are neither uniformly nor strongly asymmetrical, the writers do not believe that winter winds are sufficiently strong to account for the differences in water balance on the two slopes.

Another phenomenon associated with winter is the difference in amount of snow accumulation on the north and south slopes. A very high percentage of the snow which falls on the south slope is transferred to the north slope by wind action, even though the wind is not strong enough to distort the trees. So deep is the accumulation of snow just to the lee of the crest of Looking Glass Ridge that in places the trees exhibit an extreme degree of dwarfing and distortion (fig. 1). The lower surface temperatures on the north slope, combined with the greater accumulation of snow, enable the snow cover to linger here until very late in the spring, and as a result the season of active plant growth does not begin on the north slope until long after a comparable stage is attained on the south slope. In consequence, the critical dry season on the south slope is lengthened by a period of time equal to this difference in the initiation of vegetative activity on the two exposures. In the opinion of the writers such a difference in the length of the season of cumulative drought, during which plants are active yet must rely almost entirely upon soil moisture accumulated during the winter, constitutes the only influence sufficiently great to be commensurate with the pronounced differences in vegetation on the two slopes.

SUMMARY

Plant succession is described on talus slopes on the north and south faces of an east-west ridge in northern Idaho. Although the two areas studied are located very close to each other and at approximately the same elevation,

the environments differ so greatly that the processes of vegetational invasion, the seral communities involved, and the climax communities attained on each are strikingly different. The relative dryness so evident on the south slope is attributed primarily to the fact that the scanty snow accumulation operating together with high surface temperatures greatly advances the inception of the growing season here, and as a result the season when temperature is favorable for growth is so long that soil moisture reserves are exhausted before the summer is over.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 5, pp. 481–488 SEPTEMBER, 1943

FLOATING MATS ON A SOUTHEASTERN COASTAL PLAIN RESERVOIR

KENNETH W. HUNT

INTRODUCTION

It has been shown that a controlling factor in the vegetation of the Southeastern Coastal Plain is the widely fluctuating water table of this flat, poorly-drained region (3, 5). Most of the coastal plain "ponds" are not permanent bodies of water, and therefore do not maintain a marsh vegetation such as is seen in the north. Instead, they are invaded during the occasional prolonged periods of drought by the woody plants of the shrub-bog community, which then remain throughout subsequent fluctuations of the water table (1, 4).

This raises the question of what the vegetation would be on a pond or reservoir of this region with a sufficiently constant water supply to prevent the shrub-bog development. Some evidence in regard to this question is to be found in the floating mats on the Goose Creek Reservoir, near Charleston, S. C., which are described herein. Results of inquiry on the part of the writer indicate that this is not a solitary case. Reports have been received of floating mats on "ponds" in Accomac, Nottaway, Charles City, and James City counties, Virginia; on a mill pond at Florence, S. C.; on a reservoir at Orangeburg, S. C.; and on natural lakes at White Springs, Orange Lake, Leesburg, McIntosh, and Apopka, Florida. (Assurance was given that these Florida localities display not merely water hyacinth, *Eichhornia crassipes* Solms, but true mats supporting trees and shrubs.) The writer will appreciate reports of any other examples, even though it may not be possible to visit any of these under present war circumstances.

Although reservoirs are scarce on the sparsely populated coastal plain, it may be expected that more will be provided if the industrial development of the Southeast gets under way. The recently completed Santee-Cooper Power Development on the South Carolina coastal plain provides 165,000 acres in two permanent reservoirs, which finished filling in September, 1942. (*Alternanthera philoxeroides*[1] is already widespread in the upper Santee reservoir.) Along several of the arms of these reservoirs the U. S. Fish and Wildlife Service has constructed four Refuge Impoundments with stabilized water levels, to be stocked with marsh plants selected for their wildlife food value. At other points along the shores of the reservoir the Health and Sanitation Division of the South Carolina Public Service Authority is engaged in

[1] Authorities for all plant names mentioned are cited subsequently in the list of species collected.

restricting the vegetation for the purpose of malaria control. For these and other reasons, a knowledge of the vegetation which would normally develop on permanent coastal plain bodies of water should be of practical as well as academic interest.

DESCRIPTION OF THE GOOSE CREEK RESERVOIR

The Goose Creek Reservoir was formed in 1903 when the creek was dammed at a point 12 miles north of Charleston. This caused inundation of old sea-level rice fields which had reverted to brackish marsh. The reservoir

TABLE 1.* *Hydrogen-ion concentration of Goose Creek Reservoir, colorimetrically determined.*

Before construction of the Edisto tunnel						Since construction of the tunnel	
1923	6.6	1928	6.6	1933	5.9	1938	7.1
1924	6.3	1929	6.4	1934	6.0	1939	7.0
1925	6.5	1930	6.2	1935	5.9	1940	6.5
1926	6.7	1931	6.1	1936	6.1	1941	6.4
1927	6.8	1932	6.1	1937	6.0		
Average, 1923–1937: 6.3						Average, 1938–1941: 6.8	

* Arranged from 23rd Annual Report, Commissioners of Public Works, Water Department, Charleston, S. C.

TABLE 2.* *Mineral analyses, raw water (parts per million).*

	December 1, 1936	November 28, 1939	
	Goose Creek (Only supply)	Goose Creek	Edisto River
Sodium	7.56	9.83	6.19
Potassium	Trace	0.64	0.64
Magnesium	2.83	1.42	0.55
Calcium	3.25	4.00	2.00
Iron	0.75	0.80	0.70
Aluminum	0.07	0.40	0.51
Chloride	16.00	14.00	6.00
Sulphate	0.90	4.11	3.29
Insoluble matter	0.30		
Loss on ignition	30.00	38.00	14.50
Bicarbonate		17.08	12.20

* Arranged from 23rd Annual Report, Commissioners of Public Works, Water Department, Charleston, S. C.

is shaped like a question-mark, with a course 10 miles long and a maximum width of five-eighths mile near the lower end. The area comprises 2150 acres, inundated to an average depth of 4 feet. The upper half of the reservoir is almost wholly covered with floating vegetation. In the lower half the floating mats conceal perhaps one-third of the surface (figs. 1, 4); some lobes nearly meet in the center of the reservoir, but are prevented from doing so by a

perceptible current. Much of the mat is composed of cat-tails, but over extensive areas shrubs and trees have become established. Occasionally during storms portions of the mats are torn loose, and islands with small trees upon them have been reported sailing down the middle or across to the opposite shore (fig. 3).

The vegetation was given an early start within a year after construction of the reservoir when large masses of partially decayed roots and humus rose to the surface. Upon this support a growing mat was quickly established, and though acres of it were removed by the engineers, its growth continued. Meanwhile mats began creeping out from the shores. By 1923 it was necessary to remove some 50 acres of vegetation from the lower end of the reservoir to keep the intake clear.

The average pH value of the reservoir water, based on yearly figures from 1923 through 1937, was 6.3. In 1937 the Edisto tunnel was completed through 23 miles of marl, bringing water from the Edisto River into the reservoir. As a result of contact with the freshly-cut marl, the new water supply was alkaline, the net pH value in the reservoir rising to 7.1 in 1938, but it has now dropped back nearly to the former average (table 1). Mineral analyses are supplied separately for Goose Creek water and Edisto River water (table 2).

There was no material depletion of the reservoir until the period from 1916 through 1918, when storm damages, drought, and extra water requirements during the war combined to wholly empty the reservoir by November, 1918. (By the following January the level was again half normal.) Partial depletion recurred in 1927 and 1932. Since the opening of the Edisto tunnel in 1937 there has been not over 6 inches depletion.

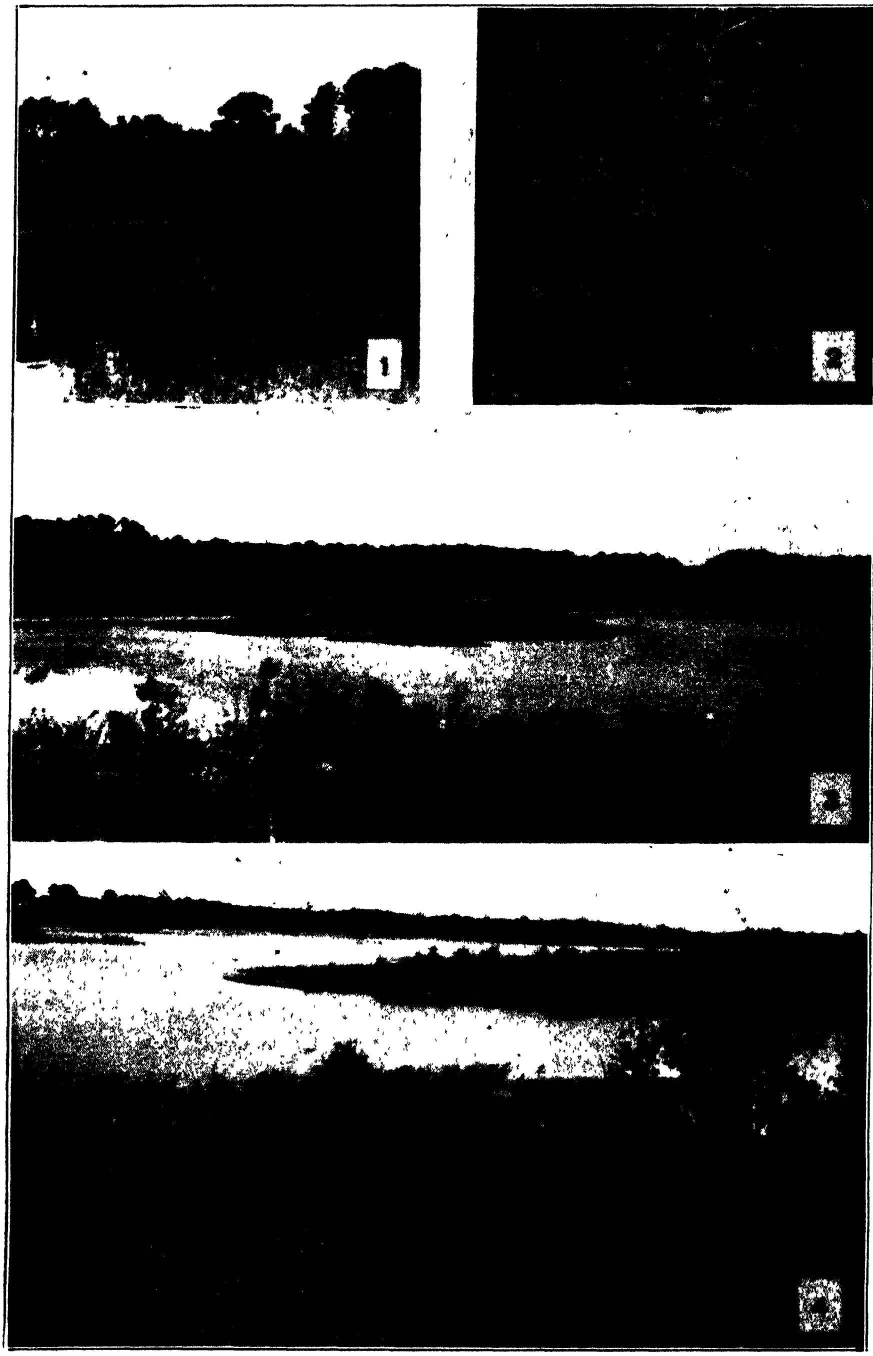
DESCRIPTION OF THE VEGETATION

The general aspect, as one looks from the water over the mats and sees successively knot-weed (*Polygonum*), cat-tail (*Typha*), and willow (*Salix*), is that of the marsh stage in the northern pond hydrosere. Closer inspection reveals that some of the main body is reaching the forest stage, and that a third of the species on the mats are plants restricted to the coastal plain from New Jersey southward. In the pioneer zone, most of the plants are southern,

---

Explanation of figures 1–4

FIG. 1. Development of a floating mat from the shore of the reservoir, showing the pioneer zone, cat-tail zone, and shrub zone. FIG. 2. *Jussiaea grandiflora* of the pioneer zone, photographed from a distance of 5 feet. FIG. 3. View taken in late winter. In the middle distance is a floating island mat, on which are discernible the pioneer zone, the cat-tail zone (lighter strip), and the main body. FIG. 4. View over the main body of a mat, taken from a cypress near its center. This mat has been partially disrupted, with loss of the cat-tail zone. In the middle distance is another floating mat. Note the trees on both mats.



and the two dominants, *Jussiaea grandiflora* and *Alternanthera philoxeroides,* are species not seen north of North Carolina.

1. Pioneer Zone. This zone averages perhaps 50 feet in width. The foremost pioneer is *Jussiaea grandiflora,* a dimorphic plant, with floating stems bearing oval glabrous leaves at the very fringe of the mat, succeeded farther back by upright branches bearing linear hirsute leaves (figs. 1, 2). In some places the advance position is locally usurped by *Hydrocotyle ranunculoides. Alternanthera philoxeroides* reaches nearly to the fringe, and together with *Jussiaea grandiflora* forms the warp and woof of the mat, the base upon which the cat-tails later start. Interwoven to a lesser extent are *Polygonum densiflorum, Polygonum acre,* and a grass, *Sacciolepis striata.* Annuals which grow upon this support are *Bidens laevis, Boehmeria cylindrica,* and *Habenaria repens.*

2, 3. Cat-tail Zone and Shrub Zone. The cat-tail zone varies from 25 to several hundred feet in width. The solid expanse of *Typha latifolia* is varied only by occasional plants of *Kosteletzkya virginica.* Intervening between this and the main body of the mat is a narrow shrub zone of scattered *Salix nigra* interspersed with abundant *Myrica cerifera.*

4. Main Body. The main body of the floating mat displays a varied flora, and is reaching the forest stage of its succession. *Acer rubrum* is frequent, with occasional specimens of *Persea pubescens* and *Taxodium distichum.* Beneath these trees and the accompanying shrubs are several species of ferns and herbaceous flowering plants, usually growing upon a thick base of *Sphagnum.* Here and there portions of the mat have sunk too rapidly, with destruction of the woody plants. This sinking occurs during the winter, when some of the vegetation dies back. Some of these areas have been filled in with a dense growth of *Panicum virgatum* and *Rubus betulifolius.* Others have a more varied flora, including several annuals, and dense growths of such vines as *Apios tuberosa* and *Mikania scandens. Decodon verticillatus,* the familiar pioneer in northern bogs, occurs in these interior open areas, but only in minor degree. Where open water occurs in the sunken areas it supports a growth of *Azolla caroliniana, Wolffiella floridana,* and occasionally *Limnobium Spongia.*

These four zones are by no means evenly developed. At some places what is designated as the "main body" is lacking (fig. 1). Elsewhere, probably owing to disruption by storms, the cat-tail zone is lacking, and a narrow pioneer zone appears to be making a fresh start directly from the shrub zone (fig. 4).

The plants in the following list were identified from reservoir specimens now filed in the College of Charleston herbarium. The collections were made on Aug. 30, 1941, March 7, 1942, May 9, 1942, July 11, 1942, and Oct.

17, 1942. Additional trips at different times and to other portions of the reservoir should add new names to the list, but it is not expected that the additions will materially affect its pattern.

The plants listed for each zone are arranged roughly in order of frequency. The letter S before a name indicates that the plant belongs to the Southern Coastal Plain and does not normally occur north of New Jersey.

PIONEER ZONE

S *Jussiaea grandiflora* Mich.
S *Alternanthera philoxeroides* Griseb.
Hydrocotyle ranunculoides L. f.
S *Polygonum densiflorum* Meisn.
Polygonum acre HBK.
S *Sacciolepis striata* (L.) Nash.
Bidens laevis (L.) BSP.
Boehmeria cylindrica (L.) Sw.
S *Habenaria repens* Nutt.

CAT-TAIL ZONE

Typha latifolia L.
Kosteletzkya virginica (L.) Presl.

SHRUB ZONE

S *Myrica cerifera* L.
Salix nigra Marsh.

MAIN BODY

Trees and shrubs

Acer rubrum L.
S *Taxodium distichum* (L.) Richard
S *Persea pubescens* (Pursh) Sarg.
Cephalanthus occidentalis L.
Sambucus canadensis L.
S *Viburnum scabrellum* (T. & G.) Chapm.
Amorpha fruticosa L.

Undergrowth

Woodwardia areolata (L.) Moore
Woodwardia virginica (L.) Small
Osmunda regalis L.
Thelypteris palustris Schott.
Sphagnum sp.
Saururus cernuus L.
Eleocharis sp.
Carex Howei Mackenzie
Galium tinctorium L.
S *Globifera umbrosa* (Walt.) J. F. Gmel.
Utricularia biflora Lam.
Lycopus rubellus Moench.
Rhus Toxicodendron L.
S *Smilax Walteri* Pursh.
S *Tillandsia usneoides* L.

Open area growth

Panicum virgatum L.
S *Rubus betulifolius* Small
Apios tuberosa Moench.
Mikania scandens (L.) Willd.
S *Ipomoea sagittata* Cav.
Cuscuta sp.
Sagittaria latifolia Willd.
S *Eleocharis ochreata* (Nees.) Steud.
Utricularia gibba L.
Hydrocotyle umbellata L.
Boehmeria cylindrica (L.) Sw.
Habenaria repens Nutt.
S *Pluchea foetida* (L.) DC.
S *Xyris communis* Kunth.
Eupatorium purpureum L.
S *Eupatorium leptophyllum* DC.
S *Ludwigia alata* Ell.
S *Hypericum petiolatum* Walt.
Hypericum virginicum L.
Hypericum mutilum L.
Cicuta Curtissii Coult. & Rose.
Ptilimnium capillaceum (Mich.) Raf.
Erechtites hieracifolia (L.) Raf.
Decodon verticillatus (L.) Ell.
S *Erianthus giganteus* (Walt.) Muhl.
Hibiscus ochroseus Britton
Solidago sp.

Pools in sunken areas

Azolla caroliniana Willd.
S *Wolffiella floridana* (J. D. Smith) Thomp.
Limnobium Spongia (Bosc.) Richard

Additional plants of the reservoir, not associated with the mats, are *Nymphaea advena* Ait., *Cabomba caroliniana* Gray, *Potamogeton pusillus* L., and abundant algal growths. *Zizaniopsis miliacea* (Michx.) Doll & Asch. grows on the bank near the intake, where the floating vegetation has been cleared away.

Wildlife is plentiful on the mats. Many species of birds are in evidence, including herons and snowy egrets. Several snakes have been seen, and abundant rabbit signs.

DISCUSSION

It is significant that the above list of plants is that of a strictly mesic succession, from marsh to incipient forest, with the xeromorphic bog stage entirely missing. It therefore cannot be compared to the floating vegetation of northern bogs, nor to the xeromorphic shrub-bog and savannah communities of the Southern Coastal Plain.

This community obviously got its start as the result of the creation of a permanent body of water. Because the bottom was never exposed to the air, except for a few weeks in the winter of 1918–1919, there was no opportunity for the development of a cypress swamp (2, 6). Neither were any of the shrub-bog plants able to invade this permanently inundated basin. But over the surface a floating community quickly developed, favored by the warm, long growing season of the southern climate. The chief pioneers, *Alternanthera philoxeroides* and *Jussiaea grandiflora*, both restricted to the coastal plain south of Virginia, made possible its rapid spread.

The real point of interest is why the succession thus initiated has never developed a bog stage. This environment differs from that of a bog in that the water is actively circulating, whereas in the bog it is comparatively motionless. Consequently this water retains its low acidity (table 1) instead of becoming highly acid as in a bog. The significance of this, and of accompanying differences in mineral content, in relation to the vegetation, constitutes matter for further study.

Meanwhile, this description of the Goose Creek vegetation may be indicative of what to expect on other permanent bodies of circulating, low-acid water created in the Southern Coastal Plain.

SUMMARY

On the Goose Creek Reservoir near Charleston, S. C., a floating mat has developed in the past forty years which is already reaching the forest stage of its succession. A list is given of 64 species collected there. Of special interest is the fact that no xeromorphic bog species are included.

This community, not previously reported for the Southeastern Coastal Plain, is believed due to the permanent presence of circulating, low-acid water in the reservoir, in contrast to the generally fluctuating high-acid water table of the region.

The vegetation on this reservoir may indicate what is to be expected when others are constructed in the Southern Coastal Plain.

The writer is indebted to Mr. J. E. Gibson, Manager and Engineer for the Charleston Commissioners of Public Works, for the information on the history of the reservoir, for permission to use the statistics shown in tables 1 and 2, and for his courtesy in making possible the collecting trips.

The writer also wishes to express thanks to Dr. B. W. Wells for his kind encouragement and helpful criticism of this report.

COLLEGE OF CHARLESTON
CHARLESTON, SOUTH CAROLINA

Literature Cited

1. **Buell, Murray F.** Peat formation in the Carolina bays. Bull. Torrey Club **66:** 483–487. 1939.
2. **Kurz, Herman & Demaree, Delzie.** Cypress buttresses and knees in relation to water and air. Ecology **15:** 36–41. 1934.
3. **Wells, B. W.** Plant communities of the coastal plain of North Carolina and their successional relations. Ecology **9:** 230–242. 1928.
4. ———. Ecological problems of the southeastern United States coastal plain. Bot. Rev. **8:** 533–561. 1942.
5. **Wells, B. W. & Shunk, I. V.** A southern upland grass-sedge bog: An ecological study. N. C. Exp. Sta. Tech. Bull. 32. 1928.
6. **Welch, Winona H.** An ecological study of the bald cypress in Indiana. Proc. Ind. Acad. **41:** 207–213. 1932.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 5, pp. 489–495 SEPTEMBER, 1943

THE INFLORESCENCE OF CRATAEGUS

H. W. RICKETT

The inflorescence of *Crataegus* is described by Fernald and Robinson (1908) and by Britton and Brown (1913) as a corymb. This term is defined by these authorities as "a flat-topped or convex open flower-cluster, in the stricter use of the word equivalent to a contracted raceme and progessing in its flowering from the margin inward;" and "a convex or flat-topped flower-cluster of the racemose type with pedicels or rays arising from different points on the axis." The second definition is more precise than the first, which even in its "stricter use" does not differentiate the corymb from the umbel and other "contracted racemes." The corymb is commonly defined in textbooks as consisting of pedicels attached along a rachis and forming a flat-topped centripetally flowering cluster. In none of the senses here expounded can the term be applied to *Crataegus*. Sargent (1905) called the flower-clusters of this genus "cymose corymbs"; which, if it means anything, presumably refers to something shaped like a corymb but blooming like a cyme—centrifugally. This, though neither a clear nor an accurate statement of the actual conditions, is a trifle nearer the truth.

This uncertainty of language reflects a current negligence in observation of inflorescences. The flowers of *Crataegus* are in a more or less "flat-topped or convex" group; their pedicels are the ultimate members of a system of some complexity. The whole answers more or less to the concept of a cyme held by Linnaeus and his contemporaries, a concept which had nothing to do with the order in which flowers open. If we are to apply the ideas implied in the definition of a cyme as a centrifugal inflorescence, it is necessary to study the compound cluster of *Crataegus* branch by branch; for certainly the inflorescence *as a whole* cannot be classified either as centrifugal or centripetal.

The clusters illustrated in figure 1 are representative of the situation in the genus so far as I have been able to study it. They were sketched from living plants near Columbia, Missouri. Though they are diagrammatic, they are approximately to scale, so that the characteristic form of the clusters is shown; the symbols by which the flowers are represented at different stages are designed to facilitate a ready grasp of the entire pattern. It is at once evident that each inflorescence is composed of a number of *unit clusters*. The latter vary in character, but a recurrent type is a simple dichasium (*a*), consisting of a short branch bearing a terminal flower and

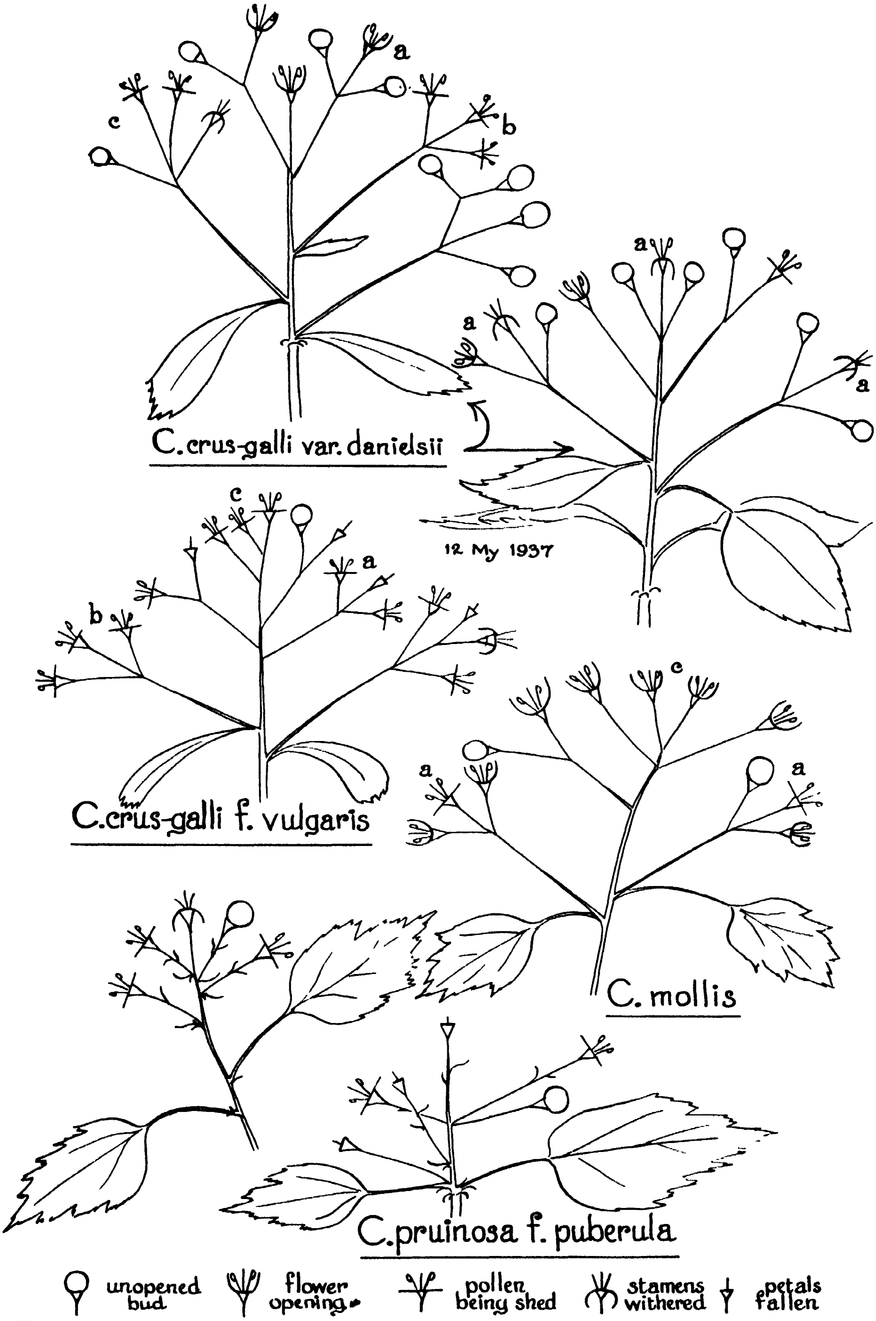
two prophylls which subtend as many lateral flowers.[1] The prophylls are early deciduous in most species; the scars left by their fall are clearly visible, but are not shown in the figure. The terminal flower frequently opens first, as in those labeled *a;* in many dichasia, however, the three flowers bloom approximately together, as at *b*.

Besides these evident dichasia are other small clusters less easy to interpret. Two-flowered branches may result from the abortion of the terminal flower or from the failure of one lateral flower to develop; the former method leads to a "false dichotomy." Irregular clusters of from three to seven flowers (*c*) may represent as many dichasia, each reduced to a single flower. That this is the most plausible interpretation appears from *C. pruinosa,* whose inflorescence is much reduced. Its prophylls (often retained during anthesis and shown in figure 1) subtend few or no lateral flowers, and each potential dichasium of this species remains commonly limited to a single flower. Some of the apparent dichasia of *C. crus-galli* also are in reality (as their bracts indicate) not so simple as they seem, but must have been formed by the condensation of a group of dichasia whose lateral flowers aborted.

In the species illustrated in figure 1 each dichasium is usually limited to three flowers; the development of new branches is not repeated from the prophylls of the lateral flowers. The repetition of the dichasial pattern, which is so familiar in (for example) the Crassulaceae, does occur in some species of *Crataegus*, such as *C. tomentosa.* The sequence is not very regular, however, and is soon lost in clusters of short-pedicelled flowers closely aggregated and blooming approximately all together.

The main branches of the inflorescence, which are thus terminated by dichasia, are aggregated in a rather irregular fashion upon a central axis. The lower branches are subtended by foliage leaves, those next above by reduced leaves which may be called bracts, the highest ones by early deciduous bracts which resemble the prophylls. One may hazard a guess that an ancestral plant bore a number of characteristic dichasial inflorescences from the axils of its foliage leaves. Such clusters would perhaps be disposed along a vegetative axis in a "racemose" fashion; i.e., those nearer the base would be better developed and would flower earlier than those towards the tip. The present inflorescence would then have originated by the condensation of the entire axis, with the reduction of most of its leaves to bracts,

[1] I use the term dichasium here in its original sense: an inflorescence which branches always "dichotomously" from beneath a terminal (often abortive) flower. Some students of today apply the term in a looser sense to refer to a cluster composed of dichasial elements, however arranged upon a main axis. As for the prophylls, this expression also I use in the common sense of the two bracts immediately below a flower which terminates a branch. They are so named by analogy, which may quite possibly be false, with the prophylls of a vegetative branch.



Explanation of figure 1

FIG. 1. Diagrams of inflorescences of several species of *Crataegus*. *a*, typical dichasia; *b*, dichasia of flowers opening simultaneously; *c*, more irregular groups.

and the aggregation of many nodes, particularly the more distal ones. Such a process must have been involved in the formation of the thyrse of *Syringa,* which is made of similar elements. Many of the "cymes" of the older botanists, such as those of *Cornus, Viburnum,* and *Sambucus,* are to be similarly understood.

A further reduction of the lateral inflorescences to one-flowered branches, as outlined above for *C. pruinosa,* would result in a characteristic corymb or raceme (in the usual sense of these terms), provided that the order of flowering of the lateral branches preserved the acropetal tendency (along the main axis) originally characteristic of their relative development. Such a mode of derivation of the racemose inflorescences has been suggested by Parkin (1914) and by Woodson (1935). In *Crataegus*, however, the various dichasia of an inflorescence bloom at approximately the same time, as is evident from figure 1. Such slight differences as appear may be in either direction. The same fact is noticed in the reduced inflorescence of *C. pruinosa.* The individual flowers of this species are disposed singly or in groups along the axis, and their flowering proceeds in various directions. The cluster may simulate a cyme, the terminal flower opening first; rarely does it suggest a corymb.

The last point introduces another potent source of confusion. A cyme is customarily defined as an inflorescence which flowers centrifugally. It has escaped the notice of many of the definition-makers that such a concept may rarely be applied to a simple inflorescence—one whose ultimate branches arise directly from a common axis—unless it consists of only a few flowers (typically three). The elementary unit from which cymose inflorescences seem to have developed is the dichasium; the development of a three-flowered into a many-flowered cluster may proceed (phylogenetically) by a repetition of dichasial branching, each new unit arising from the axil of a prophyll on a preceding dichasium, and *each dichasium flowering centrifugally.* Sometimes an inflorescence is built on pleiochasial rather than dichasial lines; there may be a whorl of branches arising from a pedicel and in turn yielding whorls of the next order. Such arrangements probably are derivative from an earlier condition. But in any case the order of flowering must be described *for each cymule;* although the entire cluster may be called cymose, it cannot be said to flower centrifugally as a whole. Only as a result of extensive reduction and condensation may it perhaps happen that a cluster is formed—as sometimes in *C. pruinosa*—which corresponds to the definition of the textbooks. The lack of attention to the above distinction is seen in the treatment of the "umbels" of *Allium* and *Pelargonium* and the "heads" of *Cornus canadensis* and *C. florida,* which (though umbels and heads are always defined as centripetally flowering) are made up of dichasial or monochasial units and flower as a whole neither centripetally nor centrifugally.

It is obvious that far too much weight has been attached in descriptive botany to the order in which flowers open. This is not a morphological character at all, nor does it correspond to any underlying morphological pattern. Flower-buds, like vegetative buds, may lie dormant; the time at which they resume growth depends on many factors. The meristematic region which ultimately becomes a lateral flower in the axil of a prophyll was derived from an apical meristem which was once at that level; the present apical meristem, which is now becoming a terminal flower some distance above the prophyll, is also descended from this same mass of

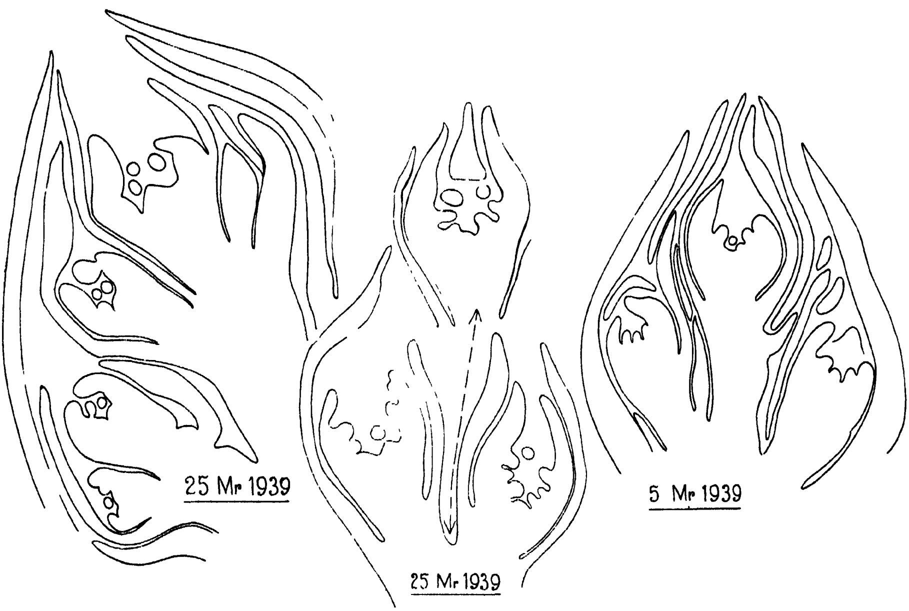


FIG. 2. Outline drawings (made with a camera lucida) of parts of sections through unexpanded inflorescences of *Crataegus crus-galli* var. *danielsii*. The central drawing is composite, since median sections of the three flowers were found in different sections; the broken line represents the attachment of the central flower, which is shown displaced.

meristematic cells. Which is the elder? If this question has an answer at all, surely the lateral meristem is older than the apical meristem above it,—irrespective of which first matures into a flower. Either may, in fact, abort.

These contentions are supported by an examination of sections through unexpanded inflorescences. Figure 2 shows portions of inflorescences of the same plant of *C. crus-galli* var. *danielsii* as is illustrated in figure 1, gathered at several dates in early spring. Terminal dichasia and parts of lateral clusters are visible. The right-hand cluster simulates a dichasium but probably (to judge from the number of bracts) is actually a cluster like the apparently simple inflorescence of *C. pruinosa*, as interpreted above. On

March 5 stamens had become evident. All the flowers, which were closely crowded, were at approximately the same stage. A parenchymatous pith is visible in the pedicels, surrounded by the provascular strands. Earlier stages are not available, but it is clear that terminal and lateral flowers of a dichasium, and even flowers representing several condensed dichasia, originate practically simultaneously from one meristem. This should be contrasted with the usual statement that the axis of a cyme is terminated by a flower, growth being continued by flowers *produced subsequently* from the axils of bracts below the terminal flower.

Sections made as late as April 1 differ little from those illustrated except for the presence of the carpels. In some dichasia the terminal flower has enlarged more than the lateral flowers; this is not always true. In the material studied (which was not as abundant as could have been wished) no difference was evident among corresponding flowers of different clusters of an inflorescence. This plant came into bloom, in the manner indicated by figure 1, during the first week in May. It is clear that the order in which the flowers open is influenced by factors which are introduced late in the ontogeny of the inflorescence and which have no necessary relation to the morphological pattern in which it was organized.

This inflorescence (and it is representative of a large number of more or less similarly derived clusters) may, as explained above, represent a half-way stage in the phylogeny of a "racemose" inflorescence; but certainly it cannot be described as a corymb. It conforms to many of the clusters called panicles, that unfortunate word having been used in such a variety of ways that it is practically useless. As Sargent saw, it is fundamentally "cymose" in pattern, and might, in fact, be conveniently referred to as a cyme, if this term is subjected to the clarification and redefinition which it needs. Since it can be shown that the introduction into morphological description of such terms as "centrifugal" and "centripetal," "determinate" and "indeterminate," rests on a wholly philosophical rather than a scientific basis, and since the order of flowering is of little value as a morphological concept, it is clear that existing definitions of cymes have a mainly historical value. I propose here to redefine a cyme as a more or less flat-topped compound cluster composed essentially of dichasia or pleiochasia (perhaps also of monochasia, since the former types grade into this in many inflorescences).[2] In this sense the inflorescence of many species of *Crataegus* (perhaps all) is a cyme; also those of *Cornus* section *Thelycrania, Viburnum,* and *Sambucus.* The recognition of the fundamental type from which a par-

[2] This is the "compound cyme" of some current workers; the "simple cyme" being what is here (and quite generally) called a dichasium. Since the cyme may be compounded in so many ways, each of which deserves analysis, it is useful to have both a general inclusive term—the cyme of the present definition—and more precise terms, such as dichasium, to indicate the elements of the composition.

ticular cyme has been derived may require close study, because of the tendency towards reduction of the dichasia or pleiochasia to one-flowered branches and the aggregation of such branches on a common axis; and because the flowers of such unit clusters frequently bloom together. Such cymes as that of *Crataegus pruinosa* can be diagnosed only by those who are familiar with the less reduced inflorescences of related species. However, it is worth while to have a definition and a concept which describe flower-clusters as they actually are, even at the cost of some trouble in applying them.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

Literature Cited

Britton, Nathaniel Lord, & Brown, Addison. 1913. An illustrated flora of the northern United States, Canada and the British Possessions. Ed. 2.

Parkin, John. 1914. The evolution of the inflorescence. Jour. Linn. Soc. **42:** 511–563.

Robinson, Benjamin Lincoln, & Fernald, Merritt Lyndon. 1908. Gray's new manual of botany. Ed. 7.

Sargent, Charles Sprague. 1905. Manual of the trees of North America.

Woodson, Robert E., Jr. 1935. Observations on the inflorescence of Apocynaceae (with special reference to the American genera of Echitoideae). Ann. Mo. Bot. Gard. **22:** 1–48.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 5, pp. 496–509 SEPTEMBER, 1943

THE CONCEPT OF INFLORESCENCE

LEON CROIZAT

In a previous article (Bot. Gaz. **103**: 771–779. 1942) the writer has reviewed some of the peculiarities of the inflorescence of the Euphorbiaceae. The present paper describes the intercalary inflorescence of certain species of the Celastraceae and Stachyuraceae, indicating generalities which pertain to the description and interpretation of inflorescences in general.

THE INTERCALARY INFLORESCENCE

In the pages of a paper currently accepted as a classic on the subject of inflorescences, Parkin states (Jour. Linn. Soc. Bot. **42**: 512. 1914): "In this paper a new term is introduced for that kind of flower-cluster, the main axis of which continues to grow vegetatively after emitting the flowers. The name *intercalary* is proposed for this."

According to this definition, an intercalary inflorescence consists of two members, both of which are essential. One, a supporting main axis (fig. 1, *a*), capable of continuing its vegetative apical growth after emitting lateral flower-clusters; the other, a certain number of flower-clusters so emitted (fig. 1, *b*). Conceived in these terms, an intercalary inflorescence can arise only on account of the interplay of a main axis with the flower-clusters which this main axis yields and supports. Naturally, the definition of such an inflorescence is essentially based on an interpretive and dynamic concept, not on a descriptive and static one. Under this concept the main axis is visualized not as a separate entity but, together with the flower-clusters which arise from it, as part of the inflorescence itself. It does not matter to the concept of intercalarity whether the main axis ceases growing immediately after emitting the last flower-cluster or beyond it, neither does it matter whether the flower-clusters themselves are cymes or racemes, many or few, simple or compound, close to or remote from the growing point of the main stem. All that matters in this concept and under this definition is the interrelation of certain branches, essentially floriferous, with an axis which is essentially sterile.

After having defined the intercalary inflorescence, stressing a dynamic and interpretative concept, Parkin adds (*op. cit.*, 514): "It seems futile to quibble over the question whether the inflorescence means the mode of floral branching or the flower-group itself. Custom has sanctioned the latter meaning." This addition is incompatible with the very definition of intercalarity, and reveals that Parkin is perhaps not master of the fundamentals of the issue with which he professes to deal. If, viewing an intercalary inflorescence,

attention is focussed *only* upon the lateral flower groups (fig. 1, *b*)—this being the "customary approach" in the sense of Parkin—the central axis (fig. 1, *a*) is bound to be neglected, which automatically destroys the perception of the factors of growth and position essential to an understanding of intercalarity. Anyone who follows the "customary approach" fails to grasp the importance of the axis that binds into a whole the flower-clusters, and, as a matter of fact, does not pay attention to this axis at all, for it is not a flower-group but essentially a vegetative shoot. Accordingly, the followers of the "customary approach" are ultimately bound to visualize the individual flower-groups as isolated cymes, racemes, spikes, and the like. In so doing they greatly narrow the scope of a study of the inflorescence in general, and are eventually thrown back upon descriptive concepts, taking up each group of flowers by itself, and attempting to define it as it looks, neglecting at the same time to take into account the main axis which is the keystone of the floriferous structure.

The voluminous literature that deals with inflorescences reveals that as a rule the approach to the problem has so far been "in the customary sense," neglecting the structural and evolutionary side of the issue, while attempting to define the various kinds of flower-clusters in a final and perfect manner. This is known to be impossible to any one who has observed inflorescences with a critical eye. Some workers, like Roeper (Linnaea **1**: 442. 1826) believed that all inflorescences could easily be segregated into two main groups ("In duas autem magnas classes omnes inflorescentiae commode distribui possunt, quarum una inflorescentias terminales vel definitas, altera inflorescentias indeterminatas vel indefinitas complectitur"), and advanced definitions which, although based on error, have unfortunately had much influence upon botanical thinking in general. Other writers, like Saint-Hilaire (Morph. Vég. 315–318. 1841) and Eichler (Blüthendiagr. **1**: 33–34. 1875), have rejected the ultimate value of the Roeperian findings, although failing to discuss them to a final conclusion. Hy's work (Rev. Gén. Bot. **6**: 385–408. 1894) lays down premises leading to numerous definitions which have never been widely accepted, and as a matter of fact are of little practical value, despite their being accurate in theory on the whole. Only twice, to the writer's knowledge, has intercalarity definitely been seen, by the brothers Bravais (Ann. Sci. Nat. II **7**: 193–221; 291–348. **8**: 11–42. 1837—see especially p. 309, 25 and footnote to p. 27, 28) and by Parkin. The findings of these workers have been ignored, however, probably on account of the obscure manner in which they were presented, and of the failure on the part of the Bravais and of Parkin to draw the necessary conclusions. To this day—much to the intuitive dissatisfaction of every thoughtful botanist—a consideration of the inflorescence generally follows the so called "customary approach," that is, emphasizes description to the ultimate detriment of inter-

pretation, stress being laid upon whether the isolated flower-cluster, for instance, is a raceme rather than a cyme or the like. Aside from the fallacy which it accepts as its main premise in theory, this approach often has catastrophic results in taxonomic practice, a student endoctrined by the "customary approach" being always baffled and bewildered by the intercalary inflorescences which he finds frequent in nature and in the herbarium.

As an illustration of the fundamental value of the concept of intercalarity for any critical study of floral axes, this writer likes to refer here to the belief of Parkin, and of Zimmermann (Bot. Centralbl. Beih. **53 A**: 95–121. 1935) that the single apical flower and the cymose raceme are the origin of all inflorescences. This theory is easily refuted. An intercalary inflorescence which is being reduced in the manner shown by figures 2–4 ultimately ends with a single apical flower, which shows that such a flower may be derivative as well as primitive. It could be objected that a derivative terminal flower is always separated from the underlying main axis by an articulation, hence that it is not truly terminal. This might be true, but is not necessarily so, because it is possible that the terminal flower arises from a central meristem, and is apical in the strict sense of the term, becoming single and articulate by abortion of the meristems lateral to it. Naturally, such a flower does not bespeak a primitive condition, since it arises by reduction of a terminal cyme. Moreover, an articulation may be so reduced as to be practically lacking, as when for instance a pad of *Opuntia* or a joint of succulent *Euphorbia* emerges from another without the intervening formation of a bud, the limits between a constriction and an articulation in the narrower sense of the term being indeed very tenuous. It is clear that the theory that the primitive inflorescence is the single apical flower and the cymose raceme primarily rests upon the loose generalizations so prevalent under the "typological approach." It is striking that neither Parkin nor Zimmermann should have felt the need to take into consideration the possible presence and significance of articulations. A stringent consideration of these peculiarities must find its place in any work that attempts to identify a rameal structure, whether primitive or derivative, sterile or floriferous.

This writer feels that too much importance is given the descriptive side of general morphology, firmly believing that this is due to subservience to frames of mind that, though valid in the days of Linnaeus, are now thoroughly dead as science. Under a normal approach to any form of biological investigation, the subject, whatever its nature, should be critically worked out before being defined, and its structural possibilities probed to the utmost before its nature, whether "cyme" or "raceme," "branch" or "leaf" is codified into words. It is difficult indeed to see a reason why botany should not follow mathematics in the use of concepts, comprehensive and often essentially undefinable, which are tested in the practical solution of problems

with absolute freedom from preliminary tiresome quibbling about definitions. It proves impossible to determine which one is the "primitive" inflorescence, whether the cyme or the raceme or the racemose cyme, for the same reason that it proves impossible to define in clean-cut terms the attributes of the absolutely primitive branch. Every discussion about primitive and derivative structures presupposes a knowledge of a starting point in evolution, and not only this, but of the tendencies that may carry a body away from such a point. Obviously, to the success of an ultimate definition a concept of motion and limits is indispensable; this, most unfortunately, would still seem to be essentially repugnant to much botanical thinking, definition and description rather than understanding and interpretation still being the main concern of such thinking. Obviously a study of phylogeny, including and aside from the inflorescence, is essentially dynamic, for it rests mainly upon an investigation of variations in structural morphology. It can be soundly argued that the primitive flower of the Euphorbiaceae has petals and sepals, and is nearest that of the Sterculiaceae and the Malvaceae, because it can be shown that that family belongs to the malvoid plexus, and has evolved in the main by suppression and modification of the organs within its flower. The case is altogether different with inflorescences in general, for in them a few basic patterns endlessly compose and decompose themselves, that which is primitive for one family being derivative for another. Academic and "typological" discussions are here useless because every case must be judged on its own merits with a broad understanding of the issue as a whole and with a mind free from the preconception, for instance, that an apple is "branch" rather than "leaf."

Recognizing the cogency of pedagogic needs and the ultimate necessity for broad definitions, this writer ventures to suggest that the theoretically primitive condition of the inflorescence is that of two meristems, one flower-bearing, the other vegetative, which meristems at the very first may be visualized as forming a dichotomous arrangement (fig. 5), only later establishing the normal anatomic and positional relationship of branch and bud. If the floral meristem in this pattern gains the ascendancy and the vegetative one develops at its side (fig. 6), a basically sympodial pattern results, which pattern is automatically reduced to one apical flower should the lateral bud fail to develop or abort. If, on the contrary, the vegetative meristem evolves first, the single lateral flower appears (fig. 7). A combination of these standard growths yields any inflorescence from the simplest to the most complex, the concept of differential growth here barely outlined applying equally well to such different axes as the single-flowered scape and the terminal woody cymose raceme. While it must be admitted that the view here advanced is essentially theoretical and pedagogical, this writer has good reason to believe that it has considerable practical bearing upon the systematic and taxonomic

interpretation of certain inflorescences in the Rubiaceae, Ranunculaceae, and Podophyllaceae, all families in which the interplay of floral and vegetative primordia is intimate and direct.

To summarize this introduction: An inflorescence is primarily to be viewed and defined as an aggregate of vegetative and floriferous axes, that is, as a structure usually (but not necessarily always) of temporary nature, brought into being, together with the flowers themselves, for the sake of reproduction. Certain elements of this structure evolve first, others later, a consideration of differential growth, *which involves both physiology and morphology,* being required for a rational treatment of all these axes. The inflorescence, consequently, answers the definition and the concept of a compound organ modified in endless details, it being futile to try to define each modification in itself and in a precise and absolute manner. The "raceme" gradually passes into the "cyme," the "single apical flower" becomes a "cluster," each one of these terms being valid as conventional description but certainly lacking the rigidity which the authors of the past have sought to impart to them. The writer does not believe that the characterization of the inflorescence which he attempts to present here is wholly above reproach, or that it can cover every detail. He feels, however, that it affords a ground of definition and elaboration which the so called "customary approach" to the study of floral axes is wholly unable to provide. Intercalarity belongs to every manner of inflorescence in principle; it is a serious error, in the considered opinion of the writer, to regard it as a special case in the life history of floriferous axes.

SOME CELASTROID INFLORESCENCES

In Rehder's excellent manual (Man. Cult. Trees & Shrubs, ed. 2, 560. 1940) the keys to cultivated *Celastrus* are based upon the characters of the inflorescence. *Celastrus scandens* L. (Waxwork or American Bittersweet) and *C. angulata* Maxim. are referred to the heading: "Fls. in a terminal panicle," while five other species including the ubiquitous *C. orbiculata* Thunb. (Oriental Bittersweet) are keyed out under the diagnostic note: "Fls. in axillary cymes often partly crowded into panicles." These definitions are empirically correct and descriptively speaking altogether sound; the coming discussion is devoted to an interpretation of the inflorescences of *C. orbiculata* and *C. scandens* in order to bring out the nature of the panicles and cymes which characterize the genus in cultivation.

1. Inflorescence of C. orbiculata. The component members of the inflorescence of this species are two, variously adapted and modified as will later be seen. One is a supporting axis ("main axis" as defined by Parkin), the other a collection of flower-clusters borne laterally and, generally, in a false apical position upon this axis (figs. 9–11). This inflorescence, consequently, is intercalary.

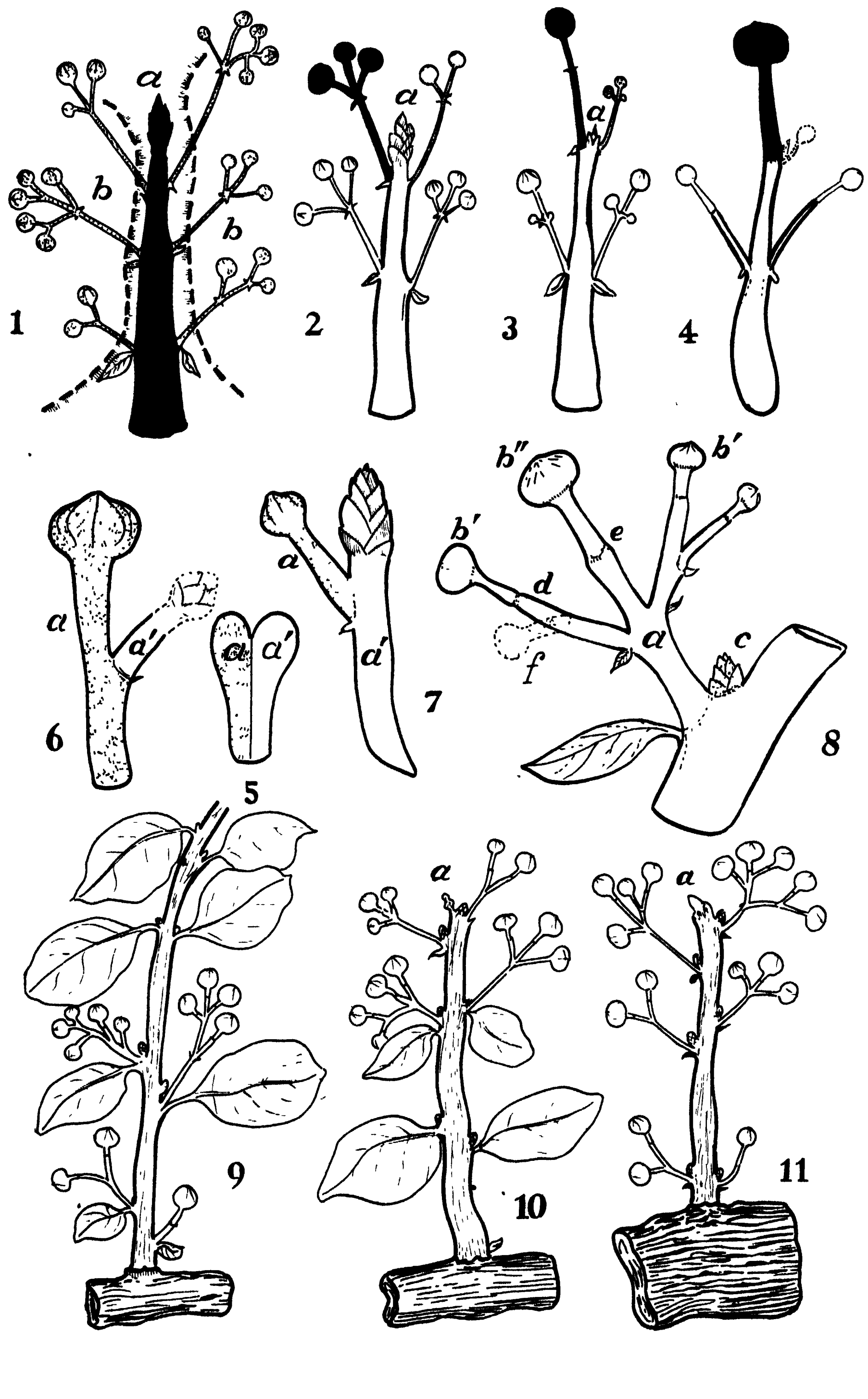
For convenience, the flower-clusters will be described here first. Each consists of an essentially cymose group of flowers which are articulate below the peduncle (that is, at the lower end of the axis which ends immediately in the flower). Omitting details, interesting as such but not to be taken up in a review of fundamentals, these clusters are arranged along the lines of the pattern shown in figure 8. The rachis of the cyme (fig. 8, *a*) emits a variable number of lateral flowers, from 1 to 7 but usually from 3 to 5, in the axils of more or less reduced bracts. Each flower so emitted may bear in its turn flowers from its pedicel. Anthesis *in the individual cluster* takes place in the conventional cymose order, or very nearly so. This means that the apical flower (fig. 8, *b″*) opens first or at least contemporaneously with the flowers which terminate the lateral secondary pedicels (fig. 8, *b′*). *Along the entire floriferous axis*, on the contrary, the time of anthesis answers the conventional definition of racemose; that is, the lower flower-clusters on the branch come into blossom first.

The articulation at the pedicel of the flower is more or less marked, being comparatively obscure (sometimes very much so) under the apical flower in a free-grown and robust flower-cluster.[1] The flower-cluster itself originates

[1] An articulation in this and similar cases generally bespeaks a time of lag or arrest in growth. A lag yields oftentimes a mere constriction; a full stop an actual or potential bud-structure. As has been pointed out elsewhere in this paper, it is not certain that constrictions and true articulations are always separable, the vigor of the shoot—in all that the term implies—having a direct bearing upon the matter. It might be added that the bud-scales show definite differential growth in certain plants (for instance, *Callistemon speciosus*, the well known "Bottle-brush"), but only arrested growth in other ones (Euphorbiaceae and Sterculiaceae in general). The time-honored argument whether the cataphyll is due to differential growth or to arrested growth can easily be settled any way a debater chooses, merely by studying certain plants in preference to others.

Explanation of figures 1–11

FIG. 1. An intercalary inflorescence and its components: *a*, supporting main axis (in the sense of Parkin); *b*, *lateral* flower-clusters. The heavy shaded line separates the two components. FIGS. 2–4. Evolution of a single terminal flower from an intercalary inflorescence; *a*, apical bud. The abortive flower and bud are merely outlined in fig. 4. FIG. 5. Floriferous (*a*) and vegetative meristem (*a′*) as the theoretical beginning of the inflorescence. FIG. 6. Condition arising from the prevalent development of the floriferous meristem. An apical flower (*a*) is established, the vegetative meristem (*a′*) yielding a lateral, ultimately sympodial arrangement. FIG. 7. Condition arising from the prevalent development of the vegetative meristem. A lateral flower (*a*) is produced, the main axis (*a′*) continuing its apical growth. FIG. 8. Lateral cymule of *Celastrus orbiculata*: *a*, rachis (main floriferous axis of the cymule); *b′*, lateral apical flowers; *b″*, central (true apical) flower; *c*, vegetative bud above cymule; *d*, flower with double articulation; *e*, normal articulation; *f*, abortive flower responsible for the double articulation at *d*. FIG. 9. Cymules absolutely lateral upon an indefinite (free-growing) sterile shoot. FIG. 10. Inflorescence derived by reduction and adaptation of the preceding; the cymules crowded in a racemose manner toward the inhibited apex of the shoot; *a*, abortive apex of the shoot. FIG. 11. Inflorescence derived by further reduction and adaptation of the two preceding; cymules borne within a leafless bracteolate raceme, often growing upon old wood (hence caulocarpic); *a*, abortive apex of the shoot.


1
2
3
4
5
6
7
8
9
10
11
a
b
a'
b'
b''
c
d
e
f

immediately below a dormant bud (fig. 8, *c*), and is subtended by a leaf or a bract.[2]

In conclusion: the lateral flower-cluster of *C. orbiculata* is to be conventionally defined as a compound cyme in a more or less advanced state of reduction. This reduction is nowhere in better evidence than upon those flowers which are borne upon an axis having a double articulation (fig. 8, *d*). This double articulation arises by elimination of a flower (fig. 8, *f*) immediately below the apical one.

The modifications undergone by the supporting main axis, that is, the branch on which the lateral flower-clusters are jointly borne ("main axis" of the intercalary inflorescence of Parkin) are fairly extensive. This branch presents three patterns in the main, as follows: (a) The branch is leafy throughout, bearing the flower-clusters mostly at the base (fig. 9); (b) The branch is leafy, sterile at the base, but toward the apex bears flower-clusters subtended by more or less evolute bracts (fig. 10); (c) The branch is much shortened, bears bracts and flower-clusters throughout, and often appears on old wood in a clear caulocarpic position (fig. 11). In this case especially, the lowermost flower-clusters may be reduced to one or two flowers.

The significance of these modifications for the usual definition of inflorescence is worth noticing and far-reaching. In the first case, the conventional student of the inflorescence merely visualizes lateral cymes borne upon a sterile shoot ("axillary cymes" of the manuals). In the second, such an observer begins to see a short branchlet ending with a racemose panicle ("flowers often partly crowded into panicles"). In the third and last case, this onlooker soars to the final perception of a full-fledged panicle. Taxonomically speaking, these visualizations are above reproach and, so far as they are descriptively intended, fairly sound. On the other hand, critically approached, all these cymes, partial racemose panicles, and full panicles are merely adaptations of the same floral pattern, that is, aspects which cannot be absolutely defined in their own right, and even less presented to the attention of a classroom without pertinent comment and elucidation. It is no less interesting to notice how taxonomists and descriptive botanists in general, being faced with concrete cases, apply the concept of intercalarity even when they are not informed of the fact that this concept has been formulated, at long last, in print. The taxonomist who describes the inflorescence of *C. orbiculata* as "axillary cymes" only sees the lateral flower-clusters,

---

[2] Although the fact has no immediate bearing upon the subject at hand, it may be mentioned here that abortive inflorescences homologous in their position with those of *Celastrus* (see *Hydrolea*, *Bougainvillea*, *Prinsepia*, *Poncirus*, and *Crataegus*) appear as thorns. Thorns of this origin and nature cannot be neglected in any exhaustive physiological and phylogenetic study of floriferous axes; their study yields in addition valuable systematic clues. Interesting investigations, so far untouched to the knowledge of the writer, await those interested in these structures and their life history.

abiding thereby by what Parkins accepts as the "customary definition of inflorescence." When this taxonomist, on the contrary, sees the flowers of the same species as being "crowded into panicles," he implicitly rejects the customary definition and accepts intercalarity as self-evident, this time visualizing *as a whole* the flower-clusters together with the "sterile shoot" which binds them. In view of this evidence, the writer needs not emphasize once again the practical value of the concept of intercalarity for a correct description and interpretation of all manner of inflorescences. The inflorescence is a prime component of much taxonomic work, which explains why authors not familiar with the workings of intercalarity happen to write laboriously and not always happily, striving to "define" floral patterns which, instead of being proteiform and confusing are indeed very simple. A great deal of useless species-making, it may be added, is to be charged to the same neglect of intercalarity.

The manner of growth of the branch which supports the lateral flower-clusters in *C. orbiculata* repays scrutiny. When it first appears this branch has a fairly definite herbaceous texture. Soon, however, it turns woody, thus shedding the usual habit of a rachis to acquire that of a true branch. As the wood matures, the dormant buds develop to the full, often even promptly bursting into growth if the growing apex of the branch happens to be cut off. Naturally, a marked difference in habit is noticeable on the same plant seen in the spring or in the fall of the year. When flowering begins, a casual observer sees "racemes" with an herbaceous green "rachis," but when the fruits are ripe, this same observer is aware only of the existence of "lateral cymes," the rachis having become by then a permanent, definitely woody branch with a manifest bark. Nothing better than this fact proves the ultimate futility of trying to define inflorescences without taking into account their life history and structural possibilities.

As has been seen, the branch which supports the lateral flower-clusters in *C. orbiculata* is usually rachis-like (figs. 12, 13), ending with an abortive tip. This abortive tip may become fused more or less extensively and intimately with the base of the nearest flower-cluster (fig. 12, *a*)[3] or stand out free (fig. 13, *a*). Under a moderate magnification this inhibited tip may be seen as surrounded by crowded bracteoles (fig. 12, *a*), or to be covered by glomerulate structures (fig. 13, *a*) suggesting flower buds. This tip, in conclusion, is vegetative or floriferous, and deciduous by an abscission layer apparently homologous with that which is active at the tip of the branchlets of *Ulmus* and *Tilia*.

[3] This type of fusion is occasional in *C. orbiculata*. It does not seem to be materially different from that which takes place in *Lilaea* (see **Campbell**, Ann. Bot. **12**: 1–28. 1898; **Arber**, Ann. Bot. II. 4: 617–627. 1940), although the fusion is much more intimate in the latter than in the former case. The writer hopes to return to the subject in dealing with prophylls and carpels.

2. Inflorescence of C. scandens. The inflorescence of the waxwork is customarily defined as a terminal panicle. It consists (fig. 14) of a rachis with a prevailing herbaceous texture, capped as a rule by an apical articulate flower, and bearing at the sides more or less numerous compound cymules. This raceme is cymose in the conventional sense because its main axis (rachis) is "definite," that is, ends with a flower. The individual flowers on this raceme, moreover, tend to open or do open cymosely, that is, the apical flower of the main axis (rachis; fig. 14, *a*) and of the lateral cymules (fig. 14, *a′*) come into blossom practically at the same time. In this respect the waxwork differs from the oriental bittersweet. In noticing the fact, the writer

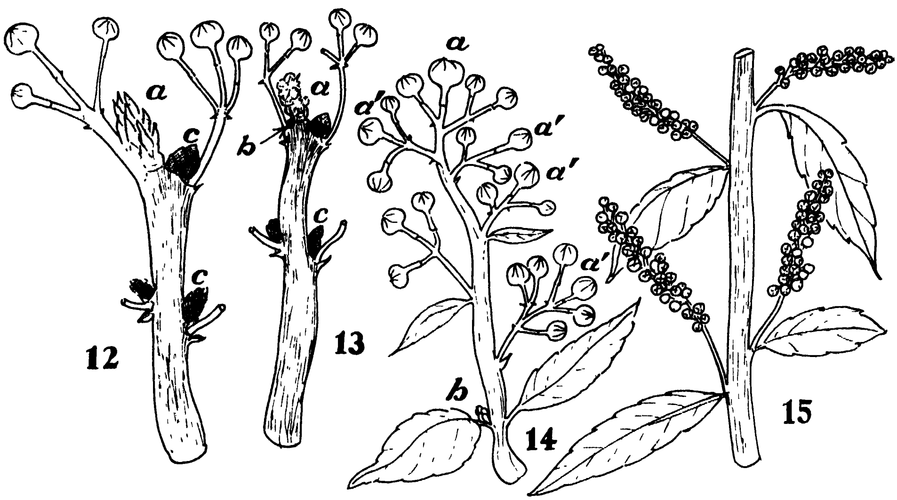


FIG. 12. Upper extremity of the inflorescence of *Celastrus orbiculata* of the pattern shown in figs. 10 and 11. The abortive (inhibited) tip (*a*), is surrounded by bracteoles (cataphylls) and tends to fuse with the base of the nearest lateral cymule. *c*, vegetative buds. FIG. 13. Same inflorescence as that shown in fig. 12. The abortive tip (*a*) is free and bears minute flower-buds. At *b* a subabortive vegetative bud, at *c* a normal one. FIG. 14. Inflorescence of *C. scandens* forming a terminal cymose raceme. *b*, growing point; *a*, *a′*, apical flowers. FIG. 15. Inflorescence of *Stachyurus yunnanensis*.

feels impelled to add that the time of opening of the flowers is not, as it has long been believed, a primary criterion by which to judge the nature of an inflorescence. Pertinent data on the causes that may influence such an opening will be read, for instance, in Stout's account of the floral behavior of the Avocado (Mem. N. Y. Bot. Gard. **7**: 145–203. 1927). This account does not support the belief that the oldest flower in a cluster necessarily blossoms first, which was accepted by Roeper as an axion in his classical but erroneous definitions.

Inflorescences of the waxwork may be found which depart from the pattern just described. This writer has collected several of them, now preserved

in the herbarium of the Arnold Arboretum. The arrangement of these inflorescences in the main is that of the bittersweet (fig. 9); that is, the flowers are borne in flower-clusters occupying a lateral position upon an otherwise freely growing branch. The leaves subtending these clusters are reduced in size, tending to become bracteal and mostly caducous. The buds that subtend the clusters are somewhat reduced and probably abortive, which is not necessarily the case with the bittersweet. The significance of this difference is not apt to be great, for the progressive abortion of apparently vegetative buds is of normal occurrence in the robust terminal panicles of certain Rutaceae (witness *Phellodendron*), and may indeed be looked for in all kinds of floriferous axes (see fig. 13, *b*). One of the abnormal inflorescences of *C. scandens* collected by this writer consists of a single lateral cymule appearing on an otherwise perfectly sterile shoot.

Viewed in its essentials, the racemo-cymose inflorescence of the waxwork (*C. scandens*) differs from the intercalary inflorescence of the bittersweet (*C. orbiculata*) in one respect only. In the latter the axis which bears flower-clusters endures as a branch throughout; in the former this axis is fully and finally adapted to floriferous functions. So far as macroscopical investigation reveals, this adaptation consists of: (1) A change in the nature and function of the axis supporting the flower-clusters. This axis, as noticed, is a true branch with normally living vegetative buds in *C. orbiculata*, a manifest rachis with abortive buds in *C. scandens;* in the former the formation of bark-tissues and secondary woody, if perhaps somewhat slowed at first, is ultimately unchecked; in the latter, on the contrary, this formation is apparently much reduced, if not actually stopped; (2) a relocation of the apical growing point. This point is located at the apex of the intercalary inflorescence in *C. orbiculata,* the main axis usually continuing its evolution in length after flower-bearing; in *C. scandens,* on the contrary, the growing point (fig. 14, *b*) is located under the "raceme." In other words and descriptively speaking, the stream of further growth runs through the inflorescence in the oriental bittersweet, but leaves it aside in the waxwork.

THE TAXONOMIC SECTIONS OF STACHYURUS

In a fundamental contribution on *Stachyurus* (Jour. Botanique **12**: 253–255. 1898), Franchet published two sections, *Callosurus* and *Gymnosurus,* which he characterized as follows: *Callosurus*—Racemes peduncled in the axil of persistent leaves; *Gymnosurus*—Racemes sessile in the axils of leaves deciduous before flowering.

The attention of this writer was invited to these characterizations by an investigator of *Stachyurus* who had found reason to suspect that Franchet's sectional key could not be properly handled unless it were elucidated beyond the usual requirements of taxonomy.

The inflorescences of *S. yunnanensis* Franch. (type-species of Sect. *Callosurus*) and *S. chinensis* Franch. (the best known species of Sect. *Gymnosurus*) revealed at a glance an intercalary tendency. In the former the laterally borne spicate racemes are subtended by a leaf of normal shape and size (fig. 15); this leaf is not affected by the evolution of the inflorescence, and persists. In the latter, the part of the branch bearing the lateral inflorescences shows an incipient specialization, so that the leaves subtending these inflorescences tend to become bracts and prove ultimately to be deciduous; this arrangement, of course, suggests a condition which may ultimately lead to the establishment of an inflorescence like that of the bittersweet (fig. 9). Understood with reference to what normally happens in intercalary inflorescences, the key of Franchet could readily be interpreted and used. This key relies at bottom upon tendencies rather than upon fixed characters. In *Stachyurus* there begins to appear a tendency toward the specialization of any shoot ("main axis" in the sense of Parkin) which happens to bear lateral inflorescences. This shoot or portion of a shoot is in its essence a full-fledged sterile axis in *S. yunnanensis;* the growth of flower-clusters upon it takes place, as it were, accidentally, without a definite interrelation being established between the shoot and the lateral inflorescence unless it be as to position, the latter happening to grow upon the former. In *S. chinensis*, on the contrary, the shoot begins to react immediately and directly to the inflorescences, its leaves behaving like deciduous bracts. A sequel to this evolution would be provided by a third species (unknown so far in *Stachyurus*) in which the shoot should become a rachis carrying a terminal thyrsoid inflorescence; this, as has been seen, being realized in *Celastrus scandens*. That the tendency toward intercalarity is barely outlined in *Stachyurus* was confirmed by the fact that certain specimens of *S. chinensis* in the herbarium retained some of their leaves even under inflorescences in full fruit. Investigation of the herbarium material available also suggested that the age of the shoot might have some influence upon the retention of the leaves. This is worth noticing, for it may be suspected that the specialization of floriferous axes, in certain cases at least, is directly influenced by the degree of maturity of the wood. In *C. orbiculata*, for instance, caulocarpic short racemes appear to be more abundant on old stems, especially at the base of the main leaders, and in other genera (*Bougainvillea, Hydrolea, Poncirus, Crataegus*, etc.) the wood of the seasonal growth bears only thorns, that is, structures which are in reality flowerless inflorescences.

SOME CONSIDERATIONS ON THE EVIDENCE

On the strength of the facts here advanced, and the conclusions which they suggest it may be stated that intercalarity is essential to an understanding of all manner of inflorescences. It may be affirmed likewise that it is

actually impossible to construct definitions to fit every kind of inflorescence. The terms raceme, cyme, panicle, thyrse, and the like have a comparatively tenuous descriptive value which, while useful, cannot afford solid and critical ground for a study of floriferous axes. This is because no real dividing-line can be drawn among these structures; it is a pure loss of time to argue, for instance, whether the inflorescence of *Sabia* is a "cyme" or a "raceme." In this genus—one among thousands—whole axillary branches, leafy at first, are turned by degrees into bracteate panicles, which in their turn become short-peduncled cymules. Mier's attempt to present an elaboration of the Winteraceae (Contr. Bot. **1**: 123–144. 1861) based in the main upon the position and the aspect of the floriferous axes is immediately seen to be radically mistaken by anyone who is informed of the fact that intercalarity is rampant in this family. In conclusion, both the morphologist and the taxonomist are bound to ease their task by accepting the fact that, while it is necessary and proper to define the inflorescence, it is even more desirable to interpret it. The sterility of much so far written on the subject, the writer believes, is due to overemphasis of the descriptive side. It is to be feared that such works as the *Philosophia botanica* of Linnaeus and the *Versuch* of Goethe have exerted an influence altogether out of proportion to their scientific value by popularizing definitions which, used in the classroom without due qualifications, have canalized the thought and the imagination of several generations of students, our own included, in a manner ultimately disturbing to free investigation. In the most definite sense these works are propaganda, for they assume as proved precisely that which stands in need of investigation, and stress the material shape of objects while obscuring their inner substance.

The attempt recently made by Grégoire (Cellule **47**: 337–339. 1938; see the discussion of *Spiraea*) to draw a sharp distinction between true branches and floriferous axes is too dogmatic, for the differences postulated by this author are invalidated in fact by the presence of endless intermediates between the extremes upon which his conclusions are made to rest. The inflorescences of *Celastrus*, no less than those of *Sabia* and countless other genera of flowering plants, furnish visual evidence to the effect that a branch, that is, a permanent woody structure, can become by degrees a rachis which is a temporary and subherbaceous organ. It may be suspected that permanency is one of the fundamental attributes of the "branch" as contrasted with other structures which happen to resemble it. Accordingly, the concept of function cannot, in this writer's firm belief, be rejected in drawing up a comprehensive and true definition of a living structure. The by now secular quibbling as to whether an apple is "branch" or "leaf" and whether a carpel "leaf" or not is promptly disposed of to the greatest benefit of morphology and botany in general by an understanding of the fact that an apple

and a carpel have functions that set them aside both from "branch" and "leaf." There can be no morphology without physiology. Grégoire's attempt at taking a dogmatic stand on the strength of laborious microscopical studies which are invalidated by direct macroscopic observation suggests that a broad familiarity with living plants is a prerequisite of ultimate specialized investigation, and that the botanical garden as an adjunct to the university has lost none of its ancient eminence. It is accepted among mathematicians that the proper statement of an equation is practically tantamount to its solution. It is not less true in botany that the proper choice of the material for investigation assures results. In voicing a criticism of certain of Grégoire's conclusions, the writer is far from associating himself with those who dismiss the work of this investigator as hardly worthy of attention and basically erroneous. Grégoire's sins of dogmaticism are less a failure of the man than of a school embracing both him and his detractors. A great deal of Grégoire's work is worthy of careful study.

SUMMARY

The intercalary inflorescence is illustrated with reference to actual structures in species of the Celastraceae and Stachyuraceae, and the value of the concept of intercalarity for an understanding of inflorescences in general is emphasized. The works of Parkin, Zimmermann, Grégoire and others are briefly noticed, and the conclusion is drawn that confusion is often made between the descriptive and the interpretive side of the study of flower-clusters.

THE ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 5, pp. 510–516 SEPTEMBER, 1943

FLOWER FORMS AND GROUPS OF DICOTYLEDONES[1]

ALFRED GUNDERSEN

HISTORICAL NOTES

The terms Dicotyledones and Monocotyledones were used by John Ray in 1703 for his subdivisions of herbaceous flowering plants. Linnaeus used these names only in classifying seeds. A. Laurent de Jussieu in 1789, the year of the French Revolution, made Acotyledones, Monocotyledones, and Dicotyledones his principal groups of plants; the last included conifers, while cycads were placed under ferns. De Candolle adopted the form Dicotyledoneae; like Jussieu, he began with Ranunculaceae. "As I find families where some of the organs become consolidated, and consequently seem to disappear. I refer them to a lower rank," he wrote. Today we would say "to a higher rank." De Candolle added "Let no one imagine I attach the least importance to the arrangement." Brongniart introduced the names Angiospermae and Gymnospermae as sub-groups of Dicotyledones. Alexander Braun in 1864 made the great improvement of subordinating Monocotyledones and Dicotyledones under Angiospermae.

Bentham had collaborated on de Candolle's *Prodromus,* and the Bentham and Hooker sequence of families of Dicotyledones closely followed that work, especially in the beginning. Their Polypetalae (1862–67) included three series with "cohorts" as follows:

I—Ranales, Parietales (incl. *Cistus* and *Papaver*), Polygalinae, Caryophyllinae (incl. *Frankenia* and *Dianthus* but not *Chenopodium*), Guttiferales, Malvales.

II—Geraniales, Olacales (incl. *Ilex*), Celastrales, Sapindales.

III—Rosales, Myrtales, Passiflorales (incl. *Cucurbita*), Ficoidales (incl. *Cactus* and *Mesembryanthemum*), and Umbellales. Polypetalae were followed by Gamopetalae and Monochlamydeae (incl. *Euphorbia*).

Eichler's *Blütendiagramme* was completed in 1878; he began dicotyledons with apetalous groups. His arrangement was approximately followed by Engler. The orders in the Engler-Diels *Syllabus* of 1936 are:

Nineteen apetalous orders, then Centrospermae (incl. *Mesembryanthemum* and *Dianthus*), then Ranales, Rhoeadales (incl. *Papaver*), Sarraceniales, Rosales, Pandales, Geraniales (incl. *Euphorbia*), Sapindales, Rhamnales, Malvales, Parietales (incl. *Cistus, Frankenia* and *Passiflora*), Opuntiales, Myrtiflorae, and Umbelliflorae, followed by Sympetalae (incl. *Cucurbita*).

[1] Brooklyn Botanic Garden Contribution No. 98.
The plates are published at the expense of the author.

Bentham and Hooker placed apetalous forms at the end, Engler at the beginning; perhaps an intermediate position may be better. Bentham and Hooker had *Dianthus* near *Frankenia,* Engler placed it near *Chenopodium;* possibly both connections may be right. Earlier botanists had *Cistus* and *Papaver* near together, but Engler placed them far apart; various recent systems have preferred the earlier arrangement.

Hallier emphasized the importance of considering all characters. Bessey, Warming, Wettstein, Hutchinson, and many others have made important suggestions.

Rendle's modification (1925) of the Engler system returns in various respects to the Bentham-Hooker arrangement. For example, *Papaver* and *Cistus* are near together; likewise *Cactus* and *Mesembryanthemum, Rosa* and *Myrtus, Passiflora* and *Cucurbita.*

Burtt-Davy (1937) considered it desirable to have a system in which orders are arranged into larger groups. His three subclasses, I. Amentiferae, II. Polystemonae, III. Oligostemonae, are divided into divisions, subdivisions, cohorts, and orders. He begins with *Garrya, Leitneria,* and *Juglans.*

DIRECTIONS OF EVOLUTION

Lotsy in 1911 wrote that so long as we do not know the origin of angiosperms a phylogenetic arrangement of the dicotyledons cannot be thought of. But according to Darrah (1939) the origin of the flowering plants is no longer "an abominable mystery," as Darwin had said, but rather an absorbing problem with many new facts at hand. H. F. Copeland wrote in 1940: "When a group is assigned to its true place, it becomes inextricable: every character studied increases the certainty of the assignment. Within a decade or two there should be few families left to be placed by guess."

We present herewith an outline of possible directions of evolution in dicotyledons; the numbers in parentheses refer to the notes which follow.

Vegetative Parts: Stem from woody to herbaceous. Vessels from scalariform to pitted (1). Leaves from evergreen to deciduous. Leaf venation from palmate to pinnate (?).

Inflorescence and Flowers: From solitary flowers to dense clusters. From large flowers to small. From convex receptacle to concave.

Sepals and Petals: From parts alike to different. From many parts to few. From separate to united (2). From spiral arrangement to cyclic (3). From regular to irregular.

Stamens: From many to few. From clustered or many to few (4). From hypogynous to epipetalous. Filament from broad to narrow. Connective from projecting to not projecting (5).

Carpels: From many to few (6). From separate to united. From ovary superior to inferior (7). Style from absent to present. Placentation from basal or parietal to apical, axile, or central (8).

Ovules and Seeds: Ovules from few to many, or to one (9). Endosperm from present to absent. Embryo from straight to curved. Seedcoats from two to one.

(1) Chalk in 1937 listed 35 families with some genera having vessels with scalariform pits; on the present charts 29 Cretaceous families are marked; ten of these are the same, namely: Magnoliaceae, Lauraceae, Hamamelidaceae, Platanaceae, Betulaceae, Fagaceae, Theaceae, Celastraceae, Cornaceae, and Caprifoliaceae. It seems certain that a great diversity of flower structures must have had a long history. (2) A majority of dicotyledons have separate petals; separate sepals are the exception and occur chiefly in the *Magnolia, Cistus,* and *Papaver* groups. (3) Sprague (1925) expresses a different idea. (4) Wilson (1942) points out that the clustered stamens, as in Tiliaceae, Hypericaceae, Myrtaceae, etc., may be the remains of former staminate branches. (5) Several conifers, *Drimys, Talauma, Platanus,* some Euphorbiaceae, *Viola, Asarum,* and also *Artemisia,* have a projecting connective; the spore-bearing part of *Ophioglossum* seems suggestive. (6) In cyclic flowers and especially in flowers in dense clusters there is not room for many carpels. (7) The close connections of Rosales to Myrtales, early fossils of Myrtaceae, Cornaceae, and Caprifoliaceae, also the otherwise primitive characters of flowers of Cactaceae, tend to reduce the importance of the character of an inferior ovary in classification. (8) Flowers with axile placentation often have parietal placentation in the bud. (9) Robinson (1904) explains polyspermy as a entomophilous character, while a single ovule often characterizes wind-pollinated plants.

GROUPS OF DICOTYLEDONES (PLATE 3)

According to Wernham (1913) and many others "Sympetalae should not exist as a separate group in a natural system of classification." This applies in all probability also to divisions such as Woody vs. Herbaceous Dicotyledones, or to Axis-flowers vs. Cup-flowers, or to Polystemonae vs. Oligostemonae. Smaller groups seem more likely to lead toward a natural classification. A number of links between families may be noted: Cistaceae→ Papaveraceae, Cactaceae, → Aizoaceae, Frankeniaceae → Caryophyllaceae, Passifloraceae→Cucurbitaceae→Aristolochiaceae, Hamamelidaceae→Betulaceae, Hamamelidaceae → Cornaceae, Euphorbiaceae → Menispermaceae, Theaceae → Cyrillaceae → Ericaceae.

Linnaeus in his *Philosophia Botanica* (1751) said that plant affinities spread out like regions on a map. At least three dimensions would seem to be necessary to indicate relationships, one for time. De Candolle said diagrams are good to explain an opinion, bad when taken as facts. Chamberlain

said a diagram is very definite, often too definite, it represents a guess at real relationships. Many diagrams of the plant world or of flowering plants have been made, for example by Giseke in 1792, by Augier in 1801, by Engler in 1897, several by Wettstein, by Bessey in 1914, by Hutchinson and by Mez in 1926, and by Tippo in 1938.

The present tentative charts and outline may be considered as a somewhat modified form of Rendle's arrangement, in part intermediate between the Bentham-Hooker and the Engler systems. But we take from Hallier, Bessey, Hutchinson, Eames and others the *Magnolia* group as the most satisfactory beginning. That need not mean it must be ancestral to all other groups.

A. Magnolia Group (Five Orders).

Flowers often large, parts separate, spiral arrangement frequent, stamens usually many, carpels often many and separate, or single.

Perianth parts separate.

Magnoliales: Magnol (*Magnolia parviflora*), Calycan (*Calycanthus floridus*), Menis (*Menispermum dahuricum*), Laurac (*Benzoin aestivale*).

Ranales: Nymph (*Nymphaea candida*), Ranun (*Trollius laxus*).

Sepals united.

Rosales (carpels separate): Rosac (*Potentilla alba*).

Hamamelidales (carpels partly separate): Hamam (*Liquidambar styraciflua*), Platan (*Platanus orientalis*).

Leguminosae (carpel single, fruit a legume): Legum (*Clitoria ternatea*).

B. Betula or Ulmus Group.

Trees or shrubs, flowers small, apetalous, sexes usually separate, stamens often in catkins, mostly wind pollination, carpels united or single, seeds usually few or one to each flower, long interval between pollination and fertilization, chalazagamy frequent. Wind-pollination is now in general not effective among the diversity of tropical vegetation, but may have been so in former ages with probably less diversity of forms. Classification not satisfactory.

Urticales: Morac (*Broussonetia papyrifera*).

Fagales (incl. *Casuarina?*): Betul (*Betula papyrifera*), Fagac (*Castanea mollissima*).

Juglandales (incl. *Myrica* and *Juliania*, all near Sapindales?): Juglan (*Juglans Sieboldiana*).

Proteales, Santalales (?).

C. Cistus Group.

Spiral or imbricate arrangement frequent, sepals usually separate, stamens often many, placentae usually parietal, that is, separate, endosperm

usually present, aril frequent, seeds usually many to each flower.

Placentation mostly parietal.

Cactales (incl. Aizoaceae with mostly axile placentation):

Cactac (*Opuntia stricta*), Aizo (*Mesembryanthemum cordifolium*).

Salicales: Salic (*Salix Caprea*).

Cistales: Cistac (*Helianthemum canum*), Tamar (*Tamarix pentandra*), Franken (*Frankenia Jamesii*).

Papaverales (mostly herbaceous, more specialized than Cistales).

Passiflorales (stamens and ovules few, incl. *Cucurbita*): Passif (*Passiflora alato-caerulea*).

Placentation axile.

Theales: Theac (*Franklinia altamaha*).

Aristolochiales: Arist (*Asarum canadense*).

Sarraceniales, near *Aristolochia* according to MacFarlane (1908).

D—I. Sepals usually united, placentation mostly axile.

D. Malva Group.

Hairs often stellate, stamens often in bundles, each carpel often one-seeded, fertilization endotropic (?), endosperm abundant.

Malvales: Tiliac (*Tilia tomentosa*), Stercul (*Theobroma Cacao*).

Euphorbiales (which families?): Euphorb (*Phyllanthus speciosus*).

E. Geranium Group.

Stamens mostly in two whorls, hypogynous, disk frequent.

Rutales (Nearly all woody plants, lvs. compound, oil glands): Rutac (*Ruta graveolens*).

Celastrales (Fls small, often 4 ptd, stamens in one whorl): Celast (*Euonymus yedoensis*).

Sapindales (characters?): Sapin (*Koelreuteria paniculata*).

Geraniales (mostly herbaceous, incl. Balsaminaceae).

F. Myrtus Group.

Calyx lobes often very small, ovary inferior.

Myrtales: Myrtac (*Myrtus communis*), Onag (*Fuchsia speciosa*).

Umbellales: Cornac (*Cornus mas*).

Garryales?

G. Dianthus Group.

Mostly herbaceous plants, stem with vascular bundles usually scattered, flowers mostly apetalous, placentation central or basal, embryo often curved.

Caryophyllales: Caryo (*Cerastium arvense*), Portul (*Portulaca grandiflora*).

Polygonales, Chenopodiales: Amaran (*Deeringia celosioides*), and perhaps Piperales.

GROUPS OF DICOTYLEDONES (PLATE 4)

Plate 4 Correction: Underline Symploc, Apocyn, Rubiac (Cretaceous).

Parts of C, E, G: the following mostly sympetalous, two staminate whorls, carpels more than two.

C. Cistus Group.

Cistales: Fouquier (*Fouquieria splendens*).

Passiflorales: Caricac (*Carica Papaya*), Cucurb (*Fevillea trilobata*).

Ebenales: Ebenac (*Diospyros Virginiana*), Sapotac (*Achras Sapota*), Symploc (*Symplocos tinctoria*).

E. Geranium Group.

Ericales: Cleth (*Clethra alnifolia*), Diapen (*Shortia galacifolia*), Epacrid (*Epacris obtusifolia*), Eric (*Erica cinerea*), Vaccin (*Vaccinium corymbosum*).

G. Dianthus Group.

Primulales: Plumbag (*Acantholimon glumaceum*), Primul (*Primula obconica*), Theophr (*Theophrasta Jussieui*).

Plantaginales (?): Plantag (*Plantago lanceolata*).

H—I. Flowers sympetalous, staminate whorl single, carpels mostly two

H. Fraxinus Group.

Many herbaceous, fls often zygomorphic, stamens epipetalous, ovary superior.

Gentianales: Apocyn (*Nerium oleander*), Asclep (*Periploca graeca*), Gentian (*Gentiana macrophylla*), Logan (*Buddleia officinalis*), Oleac (*Forsythia intermedia*).

Solanales: Solanac (*Solanum Dulcamara*), Convolv (*Ipomoea tricolor*), Gesner (*Saintpaulia ionantha*), Scrophul (*Antirrhinum majus*), Acanth (*Acanthus montanus*).

Verbenales: Borrag (*Myosotis alpestris*), Labiat (*Iboza riparia*), Polemon (*Phlox paniculata*).

I. Rubia Group.

Flowers mostly small, in dense clusters, ovary inferior.

Rubiales (many characters like Umbellales): Rubiac (*Pentas carnea*), Dipsac (*Scabiosa caucasica*).

Campanulales (flowers often large, flive carpels): Campan (*Campanula rotundifolia*), Brunon (*Brunonia australis*), Gooden (*Goodenia ovata*). Classification not satisfactory.

Asterales: Compos (*Senecio fulgens*).

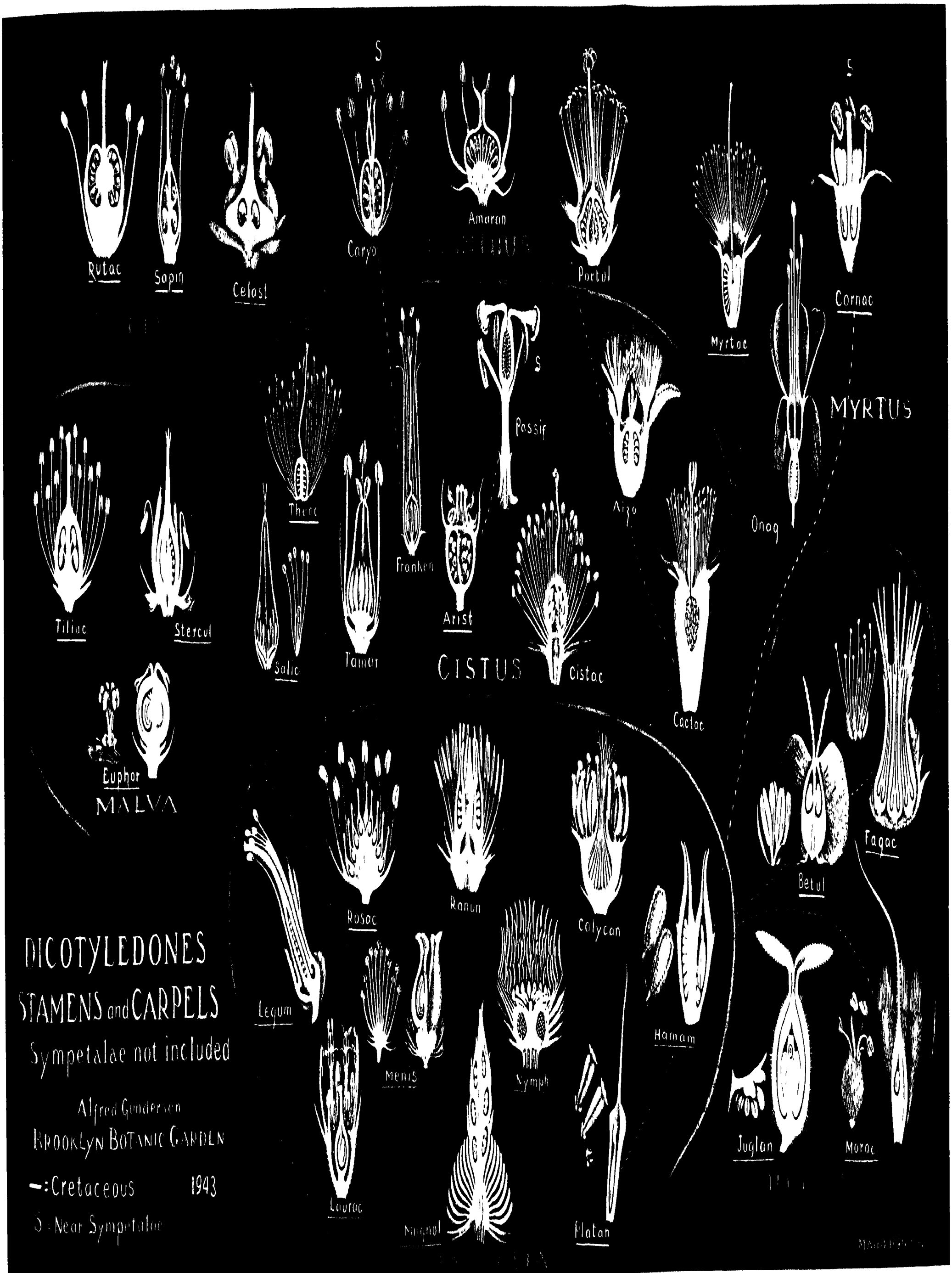
SUMMARY

This paper presents a number of problems regarding evolutionary trends in the Dicotyledones. The flower structures illustrated show facts; their arrangement ideas. As Sprague (1925) says, "until the orders themselves have been placed on a synthetic basis, no great progress can be made in the circumscription of the higher natural groups."

I wish to express my appreciation to Dr. R. W. Chaney, University of California, for information about fossil plants, and to Miss Maud H. Purdy, staff artist of the Brooklyn Botanic Garden, for the illustrations, nearly all of which were made from living plants.

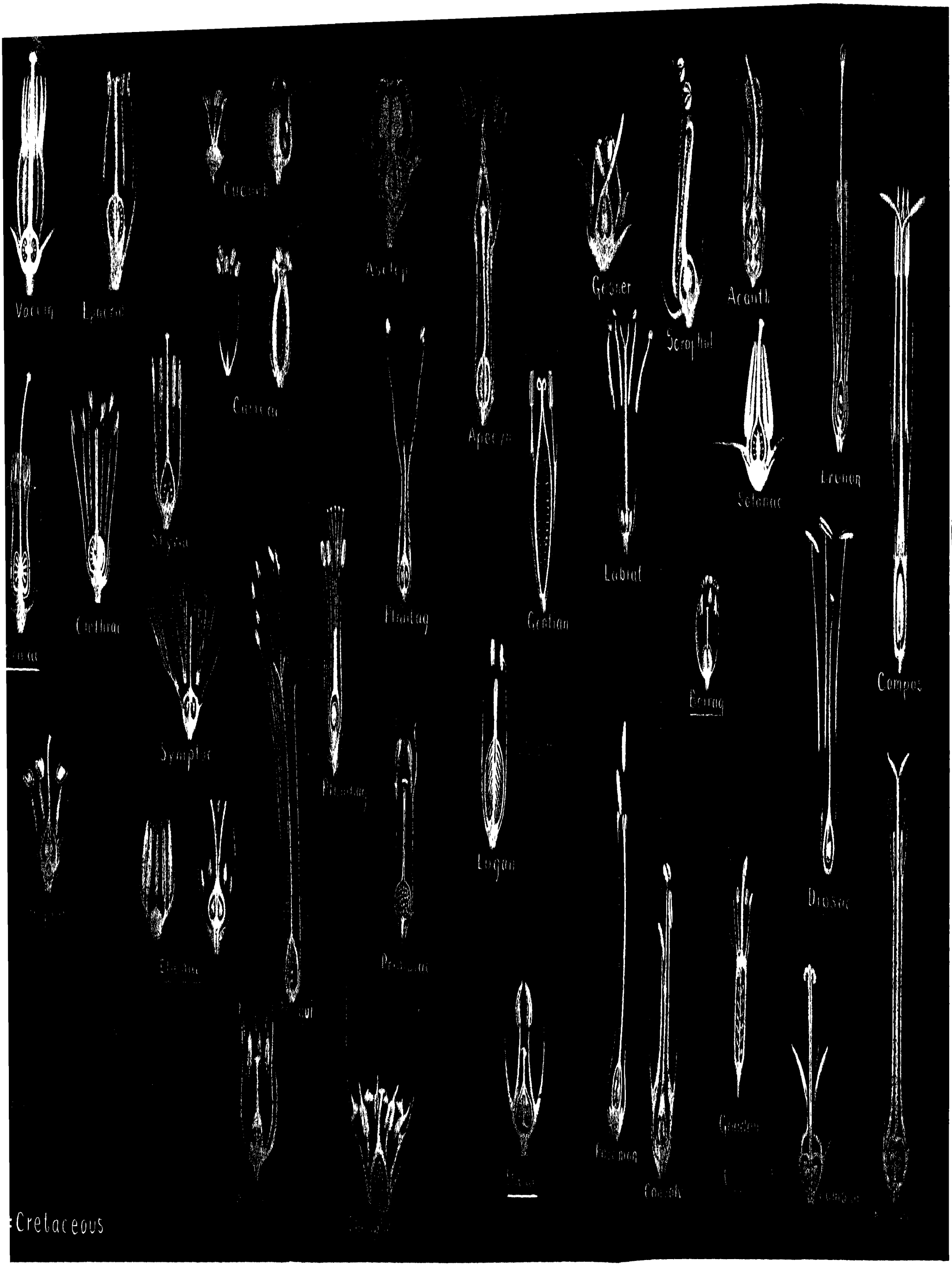
For a comprehensive list of references see Turrill, W. B. Taxonomy and phylogeny. Part III. Bot. Rev. **8**: 655–707. 1942.

BROOKLYN BOTANIC GARDEN
BROOKLYN, NEW YORK



DICOTYLEDONES
STAMENS and CARPELS
Sympetalae not included
Alfred Gundersen
BROOKLYN BOTANIC GARDEN
—: Cretaceous 1943
S - Near Sympetalae
S
Rutac
Sapin
Celast
Caryo
Amaran
Portul
Myrtac
Cornac
Passif
MYRTUS
Theac
Franken
Aizo
Onag
Tiliac
Stercul
Salic
Tamar
Arist
CISTUS
Cistac
Cactac
Euphor
MALVA
Rosac
Ranun
Calycan
Betul
Fagac
Legum
Menis
Nymph
Hamam
Juglan
Morac
Laurac
Magnol
Platan

PLATE 3



Vaccin
Gesner
Scrophul
Acanth
Apocyn
Plantag
Gentian
Labiat
Compos
Logan
Cretaceous

PLATE 4.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 5, pp. 517–530 SEPTEMBER, 1943

DESCRIPTIONS OF TROPICAL RUSTS—VI[1]

GEORGE B. CUMMINS

The Uredinales reported in this paper were collected, for the most part, by Mrs. Mary Strong Clemens in New Guinea and by C. G. Hansford in Uganda. The type specimens are deposited in the Arthur Herbarium. Specimens collected by Hansford and by Nattrass are also in the Herbarium of the Imperial Mycological Institute.

Aecidium hansfordii Cummins, sp. nov. (fig. 4). Pycniis epiphyllis, copiosis, subepidermalibus, lenticularis, 200–300 μ latis, 100–150 μ altis, sine paraphysibus. Aeciis hypophyllis, subepidermalibus, in maculis flavo-brunneis usque ad 3 cm. diam. plus minusve dense aggregatis, cupulatis, 0.15–0.25 mm. diam., margine recurvato; cellulis peridii cuboideis, ellipsoideis vel oblongis, 12–18 × 18–29 μ, pariete interiore minuteque verrucoso 3 μ cr., exteriore levi 1.5–2 μ cr.; aeciosporae globoideae, ellipsoideae vel oblongo-ellipsoideae, 12–17 × 16–20 (–23) μ; membrana hyalina, minuteque verruculosa, 1 μ cr.

On *Plectronia* (*Canthium*) *vulgaris*, UGANDA: Entebbe Road, July 1939, *C. G. Hansford 2186*, November 1940, *C. G. Hansford 2925* (TYPE).

The pycnia of this species are of striking appearance in section and appear as if stained, with the hymenial layer golden, the mass of spermatia paler, and with a clear golden-brown layer just beneath the epidermis. This layer is homogeneous, with much the color and appearance of resin and appears to be a solidified exudate of some kind.

A. hansfordii differs from *A. plectroniicola* P. Henn. and *A. incomparabile* Syd. because of the presence of pycnia and because of smaller aeciospores. *A. incomparabile* is also distinct because it causes marked hypertrophy. Other species described on *Plectronia* have the walls of the aeciospores thickened apically.

AECIDIUM HYPOESTIS Syd., on *Peristrophe* sp. (*aff. bivalvis*), NEW GUINEA: Morobe: Markham valley, Kajabit Mission, Sept. 11, 1939, *Clemens 10690*.

Dr E. D. Merrill determined the host (sterile) as follows: "Acanthaceae! and I think *Peristrophe* sp. aff. *P. bivalvis* (L.) Merr. The only other possibility is *Hypoestes* sp. but I think not."

The aecia of *A. hypoestis* are described (Ann. Myc. **29**: 175. 1931) as "aecidia pycnidia circulariter circumdantia." This is true of the smaller spots in the Clemens' collection but in older infections the aecia lack any regularity of arrangement and occur in loose groups with a diameter of as much as 1.5 cm. The pycnia mainly occur on the under side of the leaf, which is also true of Sydow's species. There appear to be no differences microscopically.

[1] Journal Paper Number 77, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany. The fifth article of this series was published in Bull. Torrey Club 70: 68–81. 1943.

A. hypoestis was described on *H. cumingiana* and *H. floribunda* from Ilocos Sur Prov., Narvacan, Philippine Islands and has not been reported from other regions.

Aecidium magnipycnium Cummins, sp. nov. Pycniis paucis, epiphyllis, profunde immersis, rufo-brunneis, 125–160 μ latis, 250–350 μ altis. Aeciis hypophyllis, in maculis flavidis usque ad 8 mm. diam. plus minusve laxe aggregatis, cupulatis vel breviter cylindraceis, albidis vel pallide flavidis, margine erosis, 0.2 mm. diam., profunde immersis; cellulis peridii oblongo-ellipsoideis, 15–22 × 26–40 μ, pariete exteriore minuteque striato 2.5–3 μ, interiore plus minusve grosseque rugoso 3 μ cr.; aeciosporae ellipsoideae vel late ellipsoideae, 15–23 × 23–30 μ; membrana 1–1.5 μ cr. vel ad apicem 2–3 μ cr., hyalina, verrucosa.

On *Clematis* sp. probably *papuasica* var. *pubescens*, NEW GUINEA: Morobe: Sattelberg, Nov. 24, 1935, *Clemens 964*, Dec. 19, 1935, *Clemens s.n.*, Mar. 4, 1936, *Clemens 1951a*, Mar. 13, 1936, *Clemens s.n.*; Yunzaing, June 29, 1936, *Clemens s.n.* (TYPE), July 16, 1936, *Clemens 3641*, Aug. 14, 1936, *Clemens 3874*; Amieng, May 8, 1941, *Clemens 12157*.

This species has characteristic long narrow pycnia which arise deep within the mesophyll, usually adjacent to the vascular elements, and extend upward to the upper epidermis. In color they are reddish brown and usually appear as if parasitized or abortive. The aecia are deep-seated also, arising just beneath the palisade layer. Not uncommonly they develop in the old pycnia and then extend almost completely through the leaf. The walls of the aeciospores are usually slightly thicker apically but this is variable.

Because of the apically thickened spores, the deep-seated sori, and especially the large pycnia *A. magnipycnium* appears not to be closely related to any rust described on *Clematis*.

Aecidium morobense Cummins, sp. nov. Pycnia amphigena, subepidermalia, conica, 100–150 μ diam., paraphysata. Aecia epiphylla, profunde immersa, non vel vix exserta, 150–250 μ diam., flavo-brunnea, in maculis rufo-brunneis leniter incrassatis usque ad 1.5 cm. diam. aggregata; cellulis peridii ellipsoideis 15–20 × 40–55 μ, membrana ubique 1.5–2 μ cr., levi; aeciosporae variabiles, praecique oblongae vel oblongo-ellipsoideae, ad apicem rotundatae, truncatae vel acuminatae, 15–26 × 35–56 μ; membrana flavo-brunnea 1.5–2 μ cr., ad apicem et basim 5–10 μ cr. et subhyalina, moderate verrucosa.

On *Elaeocarpus* sp., NEW GUINEA: Morobe: Yunzaing, Aug. 15, 1936, *Clemens 3885* (TYPE).

This species is macroscopically similar to *Aecidium elaeocarpicola* Cummins but the apically thickened spores are quite different and more like those described for *A. puspa* Racib. and *A. elaeocarpi* Racib. There is no lateral adherence into horizontal strata such as noted for *A. elaeocarpi* by both Raciborski (Bull. Acad. Sci. Cracovie Cl. Sci. Math. Nat. 1909: 276) and Cummins (Mycologia **33**: 388. 1941). The spores are also less regularly oblong, somewhat shorter, and the peridial cells are smooth. The pycnia are similar in all of these species and all cause hypertrophy of the host, but this is less pronounced in *A. morobense* and *A. elaeocarpicola* than in *A. puspa* and *A. elaeocarpi*.

There are spots on one leaf which appear to be old telia and structures were found which are probably teliospores. They measure approximately 19–21 × 50–62 μ, are ellipsoid, hyaline, and uniformly thin-walled. Unfortunately, I was unable, even in sections, to be sure that these were teliospores. If they are, as I suspect, then this species and *P. puspa* Racib. (*A. puspa*) probably have similar teliospores, although the telia of *P. puspa* occur in concentric rings rather than solitary.

Aecidium papuasicum Cummins, sp. nov. Pyeniis perpaucis, epiphyllis, profunde immersis, aureis, 130–180 μ latis, 175–200 μ altis. Aeciis hypophyllis, in maculis flavo-brunneis usque ad 1 cm. diam. laxe aggregatis, cupulatis, flavidis, profunde immersis, 225–375 μ diam., margine erosis; cellulis peridii oblongis vel ellipsoideis, 18–23 × 26–40 μ; pariete interiore moderate rugoso 2.5–3 μ cr., exteriore minuteque striato vel fere levibus 3–3.5 μ cr.; aeciosporae globoideae vel late ellipsoideae, 14–19 × 18–23 μ; membrana 1 μ cr., hyalina vel pallide flavida, minuteque verruculosa.

On *Clematis* sp. probably *papuasica*, New Guinea: Morobe: between Wareo and Sattelberg, Feb. 7–8, 1936, *Clemens 1797a;* Quembung, Mar. 2, 1936, *Clemens 2083* (TYPE).

A. papuasicum has deep-seated sori much as *A. magnipycnium* but the pycnia are somewhat smaller and more nearly globoid, the aeciospores smaller, and the spore wall uniformly thin. Macroscopically, the aecia are yellowish and bear some resemblance to the aecia of *Puccinia clavata* Syd. In *P. clavata*, however, the sori are not as deep-seated and the pycnia average only about 75 μ high and 125 μ wide.

Aecidium rutideae Cummins, sp. nov. Pycniis conspicuis, epiphyllis, subepidermalibus, lenticularis, 250–350 μ latis, 75–125 μ altis, sine paraphysibus. Aeciis hypophyllis, in maculis flavo-brunneis usque ad 2 cm. diam. plus minusve laxe aggregatis, cupulatis, margine recurvato, lacerato; cellulis peridii oblongis vel oblongo-ellipsoideis, 14–19 × 30–40 μ; pariete exteriore 2.5–3 μ cr. levi, interiore 3–4 μ cr. moderate verrucoso; aeciosporae globoideae, ellipsoideae vel oblongo-ellipsoideae, 15–23 × 20–26 μ; membrana 1 μ cr., ad apicem 3–9 μ cr., hyalina, verruculosa.

On *Rutidea rufipilis*, Uganda: Entebbe Road, August 1940, *C. G. Hansford 2785* (TYPE).

This *Aecidium*, the first described on the genus *Rutidea*, is characteristic because of the apically thickened walls of the aeciospores.

Arthuria columbiana (Kern & Whetzel) Cummins, comb. nov. (fig. 1). *Phakopsora columbiana* Kern & Whetzel, Jour. Dept. Agr. Puerto Rico **14:** 304. 1930.

A recent careful study of material of this species in the Arthur Herbarium has revealed that the urediospores are borne in chains separated by distinct intercalary cells. The rust is not, therefore, a *Phakopsora* and must be transferred to the genus *Arthuria* as the second known species. The type species, *A. catenulata* Jacks. & Holw., which also parasitizes species of *Croton*, has been reported (see Jackson, Mycologia **33:** 464. 1931) only from Brazil.

The two species are much alike but can be distinguished without difficulty in either the uredial or telial stages. In *A. catenulata* the teliospores (fig. 2) measure (18–) 20–26 × 24–35 (–40) μ while in *A. columbiana* (fig. 1) they measure (18–) 20–27 × 33–48 (–52) μ. Kern and Whetzel originally published the size of the urediospores of *A. columbiana* as 23–27 × 26–31 μ but Kern and Thurston (Mycologia **32**: 624. 1940) later increased the

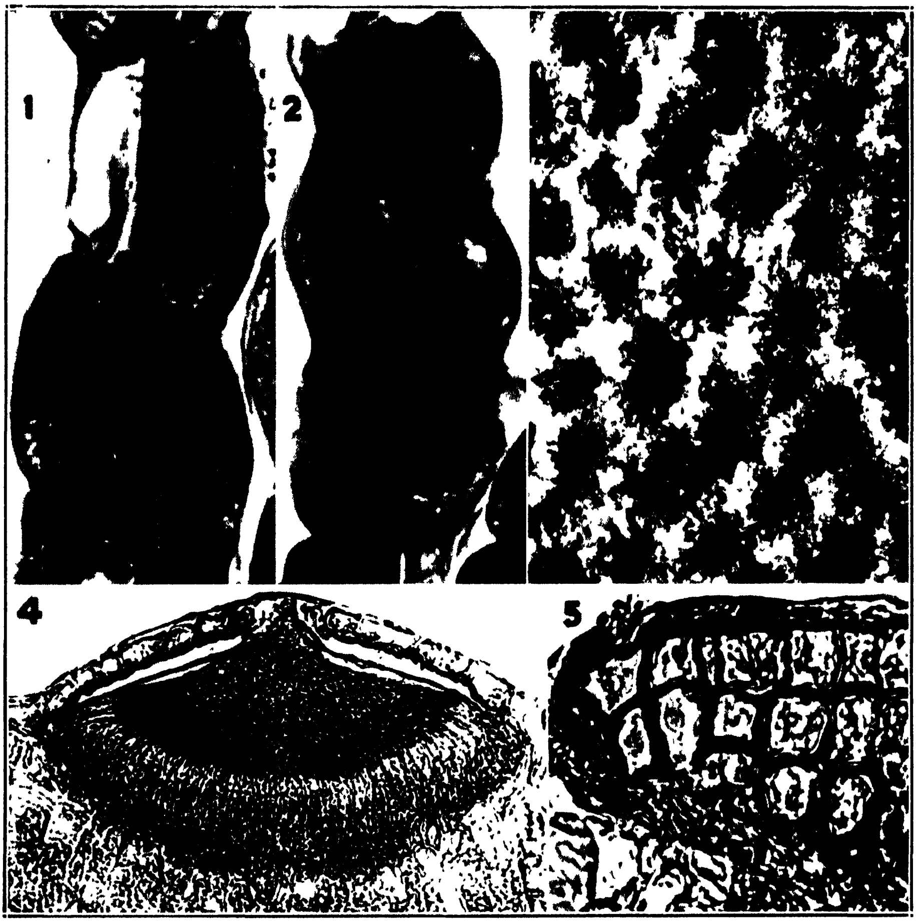


FIG. 1. Two chains of teliospores (stained) of *Arthuria columbiana;* the spores are colorless. Note that they are larger than in *A. catenulata.* (From type.) × 800. FIG. 2. Two chains of teliospores (stained) of *Arthuria catenulata;* the spores are colorless. (From type.) × 800. FIG. 3. *Cerotelium daedaloides;* surface view of a leaf showing the characteristic, labyrinthiform arrangement of the telia. The whitish lines are the telia, the dark areas are leaf surface. (From type.) × 100. FIG. 4. Freehand, unstained section of a pycnium of *Aecidium hansfordii.* The clear layer just beneath the epidermis is composed of a homogeneous, golden-brown, resin-like substance. (From type.) × 225. FIG. 5. Freehand, unstained section of a telium of *Phakopsora hansfordii.* (From type.) × 800.

measurements to 24–32 × 29–42 μ. The urediospores in both species are variable and I would give the sizes for *A. catenulata* as 18–25 × 25–35 μ and *A. columbiana* as (19–) 22–28 (–32) × (26–) 28–38 (–42) μ. There is no great difference in size but the walls of the urediospores in *A. catenulata* are only 2–3 μ thick while in *A. columbiana* they are 3–5 μ and much more coarsely aculeate. The pores are obscure in both species but are definitely scattered in *A. catenulata* and six or seven in number.

Thus far *A. columbiana* is known only on *Croton gossypifolius* from Colombia and Trinidad. The species was issued, in the uredial stage and under the name *Phakopsora crotonis,* in Reliquiae Farlowianae No. 679.

Bubakia crotonis (Cooke) Arth. (fig. 7). On October 14, 1941 telia were collected on *Croton monanthogynus* near Paoli, Indiana and overwintered at Lafayette. Seeds, collected at the same time, were used to grow plants in the greenhouse. Since early spring attempts to germinate the teliospores were negative the plants were transplanted to the garden in May and mulched with the telial material. Pycnia appeared on June 5, 1942 followed by uredinoid aecia on June 10, thus proving the species to be autoecious.

The pycnia are subcuticular, hemispherical or conical, 80–150 μ in diameter, with a delicate peridium whose apical cells become elongated and partially free but are not extruded as ostiolar filaments. The hymenial layer is flat. The aecia are uredinoid, subepidermal, without peridium or paraphyses, brownish, pulverulent, 0.2–0.7 mm. in diameter; the aeciospores are like the urediospores of the species.

While the life cycle of a species of *Bubakia* has not been completed previously by experimentation, Jackson (Mycologia **23**: 466. 1931) has described pycnia and uredinoid aecia for *B. argentinensis* (Speg.) Jacks. & Holw. on *Croton hirtus* from Brazil. Later, Cummins (Mycologia **32**: 370. 1940) also recorded pycnia and uredinoid aecia for *B. ehretiae* (Hirats.) S. Ito on *Ehretia* sp. from New Guinea.

The plants used in the experiment reported above were left until October 14, and uredia followed by telia resulted from infection by the aeciospores. Sections of the telia (fig. 7) prove that the teliospores are not catenulate but are formed by the enlargement of the individual units of a cellular tissue which underlies the sorus. At first the long axis of the developing spores is horizontal but in continued growth becomes vertical, so that the mature spores are higher than wide. As additional spores are produced they are pushed upward from the base of the sorus, or inward from the sides, and tend to be wedged between the overlying spores. A generally similar development was described (Bull. Torrey Club **67**: 69. 1940) for *B. erythroxylonis* (Graz.) Cummins and is probably characteristic for the genus.

Cerotelium daedaloides Cummins, sp. nov. (fig. 3). Pycniis, aeciis et urediis ignotis, verisimiliter nullis. Teliis hypophyllis, subepidermalibus,

erumpentibus, in maculis flavo-brunneis plus minusve indeterminatis usque ad 6 cm. longis dense aggregatis, labyrinthiformiter confluentibus, cinereo-albidis, minutis; teliosporis 4–6 superpositis, lateraliter conjunctis, plus minusve cuboideis, 7–9 × 9–13 μ; membrana ubique 0.5 μ cr., hyalina, poris germinationis verisimiliter nullis, statim germinantes ad apicem in promycelium typicum; basidiosporae ellipsoideae, 3–4 × 5–6 μ.

On *Clerodendron* sp. *aff. bucholtzii*, UGANDA: Entebbe Road, November 1940, *C. G. Hansford 2917;* on *Clerodendron* sp., Entebbe Road, December 1940, *C. G. Hansford 2939* (TYPE).

This is an interesting species of uncertain relationship. The sori are initiated beneath the epidermis but early become exposed. Individually they are minute and so densely crowded that the infected spots appear to be uniformly covered with a whitish bloom. Moderate magnification (fig. 3) reveals, however, that the sori are irregularly confluent in a labyrinthiform pattern with somewhat the aspect of the pore surface of a *Daedalia*. The lines of sori are somewhat felty due to the abundance of basidia, which are formed by the apical growth of the walls of the teliospores. The basidia are four-celled, measure about 8 × 20 μ, and produce four very small basidiospores on short sterigmata.

The species is probably microcyclic and is perhaps best referred to *Cerotelium*, a genus in which microcyclic species have not been recorded. In *Cerotelium* the teliospores are in more definite chains than seems to be true in this rust. The same is true of *Chrysomyxa*, a genus usually considered to be restricted to ericaceous hosts. Moreover, the teliospores, basidia, and basidiospores are smaller in *C. daedaloides* than in *Chrysomyxa* and there is no indication that the telia are waxy in character. In section the telia appear much like those of *C. morobeanum* Cummins (Mycologia **33**: 145. 1941, fig. 1), on *Derris*, and the teliospores are of the same size but the sori are of entirely different arrangement and gross appearance.

Hemileia harunganae Cummins, sp. nov. Pycniis, aeciis et teliis adhuc ignotis. Urediis hypophyllis, sparsis vel laxe aggregatis, pallide flavidis, minutissimis, per stomata erumpentibus; urediosporae ellipsoideae vel globoideae, 16–23 × 19–25 μ; membrana 1.5–2 μ cr., pallide flavida vel fere hyalina, denseque echinulata; poris germ. obscuris.

On *Harungana* (*Haronga*) *madagascariensis*, UGANDA: Kawanda, August 1940, *C. G. Hansford 2803* (TYPE).

This is the first record of a species of *Hemileia* on Hypericineae.

Hemileia rutideae Cummins, sp. nov. Pycniis et aeciis incertis. Urediis hypophyllis, partes foliorum plus minusve dense obtegentibus vel sparsis, minutissimis, flavidis, per stomata erumpentibus; urediosporis in apice hypharum fasciculatim erumpentium ortis, plus minusve reniformis, 19–23 × 26–35 μ; membrana hyalina vel pallide flavida, in parte superiore 2–3 μ cr. moderate aculeata (1.5–3 μ), inferiore 1.5 μ cr. frequenter fere levibus; poris germ. obscuris. Teliis adhuc ignotis.

On *Rutidea rufipilis*, UGANDA: Entebbe Road, November 1940, *C. G. Hansford 2915* (TYPE).

There are remnants of old aecial infections on two leaves of this collection. These may have been caused by *Aecidium rutideae*, which was collected on the same host in this locality.

Phakopsora hansfordii Cummins, sp. nov. (figs. 5, 6). Pycniis et aeciis ignotis. Urediis hypophyllis, sparsis vel laxe aggregatis, rotundatis, 75–175 µ diam., pallide brunneis, subepidermalibus; paraphysibus periphericis, copiosis, incurvatis, plus minusve clavatis, 10–14 × 23–55 µ, lumine nullo vel subnullo; urediosporae obovoideae vel ellipsoideae, 15–19 × 23–30 µ; membrana 1–1.5 µ cr., minuteque echinulata, flavo-brunnea vel pallide cinnamomea; poris germ. obscuris. Teliis hypophyllis, in maculis flavidis vel brunneis laxe aggregatis vel sparsis, rotundatis vel irregularibus, 0.1–0.5 mm. longis, subepidermalibus, indehiscentibus, atro-brunneis; teliosporis 2–6 superpositis, oblongis, cuboideis vel plus minusve ellipsoideis, 8–18 × 14–23 µ; membrana ubique 1 µ crassa, aureo-brunnea.

On *Alcornea cordifolia*, UGANDA: Kawanda, March 1940, *C. G. Hansford 2561* (TYPE).

The uredial paraphyses (fig. 6) provide the distinguishing feature of this species. They are composed of a short, thin-walled stalk and an irregular club-like upper portion which appears to be solid. This upper portion is highly refractive to light, when mounted in water, and appears as it might if densely filled with protoplasm. When mounted in glycerine-alcohol the upper portion loses its refractive appearance. Macroscopically, the paraphyses appear as a whitish ring about the sorus.

The uredia and telia both develop directly below the epidermis from a flat sporogenous layer and do not extend into the mesophyll.

PHAKOPSORA MEIBOMIAE Arth., on *Desmodium* sp., NEW GUINEA: Morobe: Malalo Mission, May 25–27, 1936, *Clemens 3111a*, Amieng, Feb. 14, 1941, *Clemens 11887*; on *Uraria lagopodioides*, Kajabit, Aug. 2, 1939, *Clemens s.n.*

This species has not been recorded for New Guinea previously, although reported from the Philippines. The collection on *Uraria* is referred here tentatively since the uredia are like those of *P. meibomiae*. Species of *Uraria* have not been reported as hosts for species of the Uredinales.

PHAKOPSORA VIGNAE (Bres.) Arth., on *Phaseolus lunatus*, NEW GUINEA: Morobe: Boana, May 23, 1940, *Clemens s.n.*

Although Hiratsuka (Bot. Mag. Tokyo **49**: 786. 1935) treats this rust as a synonym of *P. pachyrhizi* Syd. I have pointed out recently (Bull. Torrey Club **70**: 73 1943) that there is some evidence that this may not be correct. *P. pachyrhizi* has been reported from New Guinea on *Mucuna* but this is the first account of the occurrence of *P. vignae*. Telia are not present in either specimen.

PUCCINIA GOUANIAE-TILIAEFOLIAE Syd., on *Gouania* cf. *javanica*, NEW GUINEA: Morobe: Boana, Oct. 8, 1940, *Clemens s.n.*

This species, described from the Philippines, has not been recorded as occurring in New Guinea.

Puccinia hansfordiana Cummins, sp. nov. (fig. 11). Pycniis et aeciis ignotis. Urediis amphigenis, subepidermalibus, sparsis, obscure cinnamomeis,

pulverulentis, rotundatis, 0.2–0.5 mm. diam.; urediosporae late ellipsoideae vel ellipsoideae, 23–26 × 28–38 μ; membrana 1.5–2 μ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 3, aequatorialibus. Teliis urediis conformibus sed pulvinatis; teliosporae ellipsoideae vel oblongo-ellipsoideae, utrinque rotundatae vel deorsum leniter attenuatae, medio leniter constrictae, 25–31 × 43–56 μ; membrana 1.5–2 μ cr., ad apicem 4–6 μ cr., castaneo-brunnea, levi, poro superiore apicali, inferiore juxta septum sito; pedicello sporam aequante vel breviore, semipersistenti, hyalino.

On *Senecio denticulatus*, UGANDA: Kachwekano Farm, Kigezi, August 1937, *C. G. Hansford 2227* (TYPE).

This rust has a general resemblance to *Puccinia senecionicola* Arth. but the apical walls of the teliospores of *P. hansfordiana* are thinner, the thickening being in the nature of a semihyaline, differentiated, unbonate cap, and the urediospores have three rather than two pores. *Uredo senecionicola* Jacks. & Holw., described from Ecuador, has similar urediospores but is probably not synonymous.

PUCCINIA OAHUENSIS E. & E., Bull. Torrey Club **22**: 435. 1895 (figs. 9, 10). (*Uredo digitariaecola* Thüm., Myc. Univ. No. 2041. 1882; *Puccinia digitariae* Pole Evans, Ann. Bolus Herb. **2**: 111. 1917.)

P. oahuensis has been considered to occur only in Hawaii (see Stevens, Bernice P. Bishop Mus. Bull. **19**: 122. 1925). There are, in the Arthur Herbarium, Puerto Rican specimens which bear this name but they were never reported in print as such and were included under *P.* (*Dicaeoma*) *tubulosa* in the North American Flora. Arthur and Cummins (Phil. Jour. Sci. **59**: 439. 1936) reported *P. paspalicola* (*P. tubulosa*) from the Philippines and Cummins (Mycologia **33**: 147. 1941, with fig. 3) reported similar New Guinea collections as *P. digitariae*. In neither case was *P. oahuensis* given consideration, although the New Guinea collection occurs on the same host, *D. pruriens*. Hiratsuka (Bot. Mag. Tokyo **59**: 20. 1935) has recognized *P. oahuensis* on four species of *Digitaria* (*Syntherisma*) in Formosa, as well as for various localities in other publications. The African *Puccinia* on *Digitaria* has been referred to *P. digitariae* (Sydow, Monogr. Ured. **4**: 604. 1924; Doidge, Bothalia **2**: 124. 1927, with fig.; **3**: 499. 1939, with fig. 16; Hopkins, Trans. Rhod. Sci. Assoc. **35**: 106. 1938; Dade, Bull. Misc. Inf. Kew **1940**: 219. 1940).

Through the courtesy of Miss Doidge and Dr. Bisby representative collections of the African rust have been available for study, although I have not seen Pole Evans' type. I have been able to study telial material from Hawaii (including the type, fig. 10), the Philippines, New Guinea, India, Transvaal, Southern Rhodesia, Uganda, Brazil and Puerto Rico (fig. 9). With the possible exception of the Uganda collection the specimens appear to represent a single species. The telia are small, inconspicuous, and remain more or less indefinitely covered by the epidermis of the host. Consequently the teliospores are closely compacted and variable in size and shape. Mesospores are not uncommon, especially at the edge of the sori. At the periphery of the sorus there is a very slight development of brownish paraphyses (fig. 9, p) but the sorus is not divided into locules. The urediospores are light

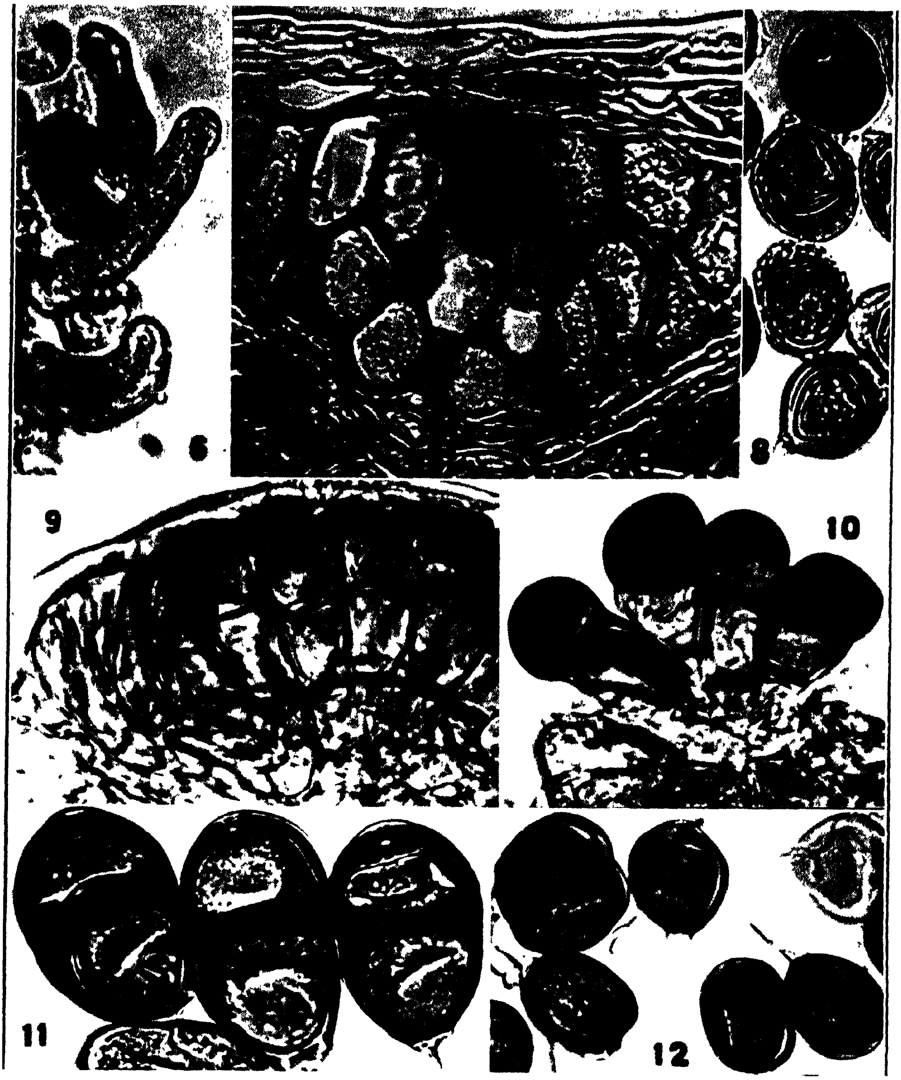


FIG. 6. Uredial paraphyses of *Phakopsora hansfordii*. (From type.) × 800. FIG. 7. Freehand, unstained section of a telium of *Bubakia crotonis*. Note that the teliospores are not arranged in chains but are produced in an irregular manner from a basal, rather thick-walled, cellular tissue which lies more or less at right angles to the long axis of the mature spores. (From culture material described in the text.) × 800. FIG. 8. Teliospores of *Uromyces pustulatus;* the spores are minutely reticulate. (From Hansford *2811*.) × 800. FIG. 9. Freehand, unstained section of a telium of *Puccinia oahuensis;* note the slight development of paraphyses at P. (From Seaver & Chardon *1415*.) × 800. FIG. 10. Teliospores of *Puccinia oahuensis*. (From type.) × 800. For illustrations of teliospores from Africa and New Guinea see references cited in the text. FIG. 11. Teliospores of *Puccinia hansfordiana*. (From type.) × 800. FIG. 12. Teliospores of *Puccinia ugandana*, a species characterized by a preponderance of mesospores. The two-celled spores are variable in size and configuration but are frequently diorchidioid, as shown here. (From type.) × 800.

cinnamon- or golden-brown, echinulate, and have four to six, usually four or five, equatorial pores. Measurements of the spores are as follows: Hawaii (type of *P. oahuensis*), II: 22–29 × 28–36 μ, III: 17-26 × 27–39 μ; Philippines (Clemens *1712*), II: 22–26 × 25–30 μ, III: 16–24 × 27–40 μ; New Guinea (Clemens *s.n.*), II: 22–28 × 28–33 μ, III: 17–23 × 28–46 μ; India (Sydow, Ured. *2272*), II: 21–26 × 26–32 μ, III: 18–26 × 36–48 μ; Transvaal (Doidge, Myc. Herb. Union Dept. Agr. *27587*), II: 23–30 × 27–36 μ, III: 14–23 × 33–50 μ; So. Rhodesia (Hopkins *2002*), II: 20–21 × 26–29 μ, III: 17–25 × 38–52 μ; Brazil (Müller *540*), II: 18–24 × 23–31 μ, III: 17–23 × 33–42 μ; Puerto Rico (Seaver & Chardon *1415*), II: 19–23 × 23–30 μ, III: 16–22 × 35–40 μ. Doidge (Bothalia **2**: 124. 1927) gives the following measurements for South African material: II: 19–24 × 23–33 μ, III: 20–30 × 27–47 μ. Sydow's (Monogr. Ured. **4**: 604. 1924) measurements for the spores found in *Uredo digitariaecola* are: II: 19-24 × 24–33 μ, III: 17–19 × 35–40 μ.

The evidence indicates that these collections of *Puccinia* on *Digitaria* represent a single species which should be designated as *P. oahuensis*. *Puccinia substriata* Ellis & Barth. (*P. tubulosum*) (see Cummins, Mycologia **34**: 683. 1942) is not synonymous.

It was mentioned above that the Uganda specimen (Hansford *2176* on *D. scalarum*) differed somewhat from other collections. The uredia have peripheral paraphyses like those of *P. oahuensis* and, while of the same size (20–29 × 26–35 μ), the urediospores have six to eight scattered pores. The teliospores are similar also (17–24 × 38–52 μ) but the telia rupture the epidermis at an early stage of development and become quite evident. This collection may be only a variant of *P. oahuensis* or it may represent an undescribed species. I prefer to accept the first of these possibilities until additional collections become available.

Puccinia ugandana Cummins, sp. nov. (fig. 12). Pycniis, aeciis et urediis nullis. Teliis hypophyllis, subepidermalibus, in greges usque ad 4 mm. diam. dense aggregatis, soris individuis 0.2–0.5 mm. diam., castaneo-brunneis, pulvinatis; teliosporae variabiles, praecique ellipsoideae vel plus minusve diorchidiodeae, utrinque rotundatae, medio non vel leniter constrictae, 17–24 × 22–27 μ; membrana pallide castaneo-brunnea vel aureo-brunnea, levi, 2–2.5 μ cr., ad apicem 3.5–6 μ; mesosporis copiosis, ellipsoideis vel globoideis, 17–23 × 19–25 μ; pedicello persistenti, hyalino, 3–6 μ lata, sporam aequante vel longiore.

On *Jasminum* sp., UGANDA: mile 20, Horina Road, April 1940, *C. G. Hansford 2672* (TYPE).

P. ugandana is a microcyclic species, strikingly different from species of *Puccinia* previously described on Oleaceae because of the small, commonly diorchidioid teliospores and the abundance of mesospores. The mesospores are the predominant type, the two-celled spores being infrequent. Because of the small size of the mesospores they can be readily distinguished from the teliospores of *Uromyces hobsoni* Vize or *U. comedens* Syd.

PUCCINIA VAGANS (DC.) Arth., on *Epilobium* sp., NEW GUINEA: Morobe: Mt. Sarawaket, Oct. 18, 1937, *Clemens 7262.*

P. vagans has not been reported from New Guinea but is a rust of wide distribution. The collection consists of the systemic aecia which are characteristic of the species. It was collected at an estimated elevation of 10,000 ft.

RAVENELIA BREVISPORA Hirats. & Hash., on *Breynia?* sp., NEW GUINEA: Morobe: Kajabit Mission, July 29, 1939, September 1939, *Clemens s.n.;* on *Phyllanthus* sp., Kajabit Mission, Sept. 20, 1939, *Clemens 10700.*

Telia are not present in these collections but there are old aecial spots which may indicate that this species has cupulate aecia. Through the kindness of Dr. Hiratsuka I have been able to compare the uredia with the type of *R. brevispora* and find satisfactory agreement.

R. brevispora was described (Bot. Mag. Tokyo **49**: 522. 1935) on *Phyllanthus reticulatus* from Formosa and has not been reported previously from New Guinea.

UREDO CENCHRICOLA P. Henn., on *Cenchrus ciliaris*, UGANDA: Kawanda, March 1941, *C. G. Hansford 2987.*

While no specimen has been available for comparison I feel sure that Hansford's collections are *U. cenchricola*. The spores are large, measuring 23–29 × 29–39 (–42) μ, have a cinnamon-brown wall 2–2.5 μ in thickness, and four or five equatorial pores. The species is readily distinguishable from *Puccinia cenchri* Diet. & Holw. because of the more numerous pores.

Uredo cissicola Cummins, sp. nov. Urediis hypophyllis, rarius epiphyllis, subepidermalibus, sparsis vel laxe aggregatis, rotundatis, 0.15–0.35 mm. diam., cinnamomeo-brunneis, pulverulentis, epidermide rupta conspicue; urediosporae ellipsoideae, obovoideae vel oblongo-ellipsoideae, 19–25 × 26–35 μ; membrana 1.5 μ cr., flavidula vel fere hyalina, valde echinulata; poris germ. obscuris.

On *Cissus quadrangularis*, UGANDA: Kiterera, Busoga, September 1940, *C. G. Hansford 2813* (TYPE).

U. cissicola is characterized by relatively large, sharply echinulate urediospores and sori devoid of paraphyses, features which distinguish it from previously described rusts on Vitaceae.

Uredo entandophragmae Cummins, sp. nov. Urediis hypophyllis, subepidermalibus, pustulatis, rotundatis, 0.1–0.3 mm. diam., brunneis; urediosporae ovoideae, obovoideae vel oblongo-ellipsoideae, 15–21 × 25–36 (–42) μ; membrana 1.5 μ cr. vel ad apicem 2–3 μ cr., pallide cinnamomeo-brunnea vel flavido-brunnea, moderate echinulata vel ad basim fere levibus; poris germ. obscuris.

On *Entandophragma* sp., UGANDA: Entebbe Road, December 1940, *C. G. Hansford 2911* (TYPE).

There is no previous record of a rust on *Entandophragma* nor is there a similar *Uredo* known on Meliaceae.

Uredo kigeziensis Cummins, sp. nov. Urediis amphigenis, subepidermalibus, sparsis vel laxe aggregatis, ovalis, ellipticis vel linearis, usque ad 1.5 mm. longis, longitudinaliter dehiscentibus, flavidis; urediosporae late ellipsoideae, ellipsoideae vel obovoideae, 14–19 × 19–26 μ; membrana 1.5 μ

cr., pallide flavida vel hyalina, densiuscule minuteque echinulata; poris germ. obscuris, verisimiliter sparsis.

On *Eragrostis macilenta*, UGANDA: Kabale, Kigezi, August 1937, *C. G. Hansford 2226* (TYPE).

Puccinia eragrostidicola Kern and *Angiopsora hiratsukae* Syd. have pale urediospores of about the same size as those of *Uredo kigeziensis* but the presence of paraphyses in their uredia is a distinguishing feature. Paraphyses are not described for *Puccinia eragrostidis* Petch but both the uredia and the urediospores are small.

UREDO MELINIDIS Kern, on *Melinis maitlandii*, UGANDA: Kawanda, June 1940, *C. G. Hansford 2727;* on *Melinis minutiflora*, SIERRA LEONE, Njala, November 28, 1930, *F. C. Deighton 335.*

This species, described from Venezuela on *M. minutiflora* and also recorded for Brazil on the same host, has not been reported previously from Africa. The type specimen has been available for comparison and the African specimens differ in no way.

Inasmuch as *Melinis minutiflora* is a native of Africa and was introduced into South America one might expect that the rust also originated in Africa. The grass occurs as a forage plant in South and Central America and the West Indies and the rust will probably be found to have a wider distribution than recorded at present.

Uredo mira Cummins, sp. nov. Urediis subepidermalibus, amphigenis, sparsis, rotundatis vel ovalis, 0.1–0.4 mm. longis, pulverulentis, castaneis, epidermide rupta conspicue, paraphysibus peripherales variabiles numerosis, plus minusve cylindraceis, 10–20 × 50–85 μ, membrana pallide flavida vel fere hyalina, 2–3 μ cr. vel ad apicem 3–30 μ; urediosporae ellipsoideae, obovoideae vel late ellipsoideae, 23–29 × (29–) 32–40 (–42) μ; membrana 2–2.5 μ cr., moderate echinulata, obscure cinnamomea vel castanea; poris germ. 3 vel rarius 4, aequatorialibus.

On *Manisuris altissima* (*M. fasciculata*), Buenos Aires, Argentina, March 1906, *R. Thaxter 63* (TYPE) (Reliq. Farl. 759 as *Puccinia levis*).

U. mira is characterized by rather large, dark brown spores and highly variable paraphyses. The paraphyses may be narrowly or broadly cylindrical or more or less bottle-shaped and may be straight or variously curved. Their walls may be uniform in thickness or greatly thickened above.

The most nearly related species is *Puccinia cacao* McAlp. (*Uredo rottboellii* Diet.). Urediospores of the two species are similar in size and pigmentation but if published descriptions are correct *P. cacao* does not form paraphyses in the uredia. *P. pappiana* Syd. on *Manisuris granularis* has capitate paraphyses and smaller urediospores.

Thaxter's specimen was mentioned by Arthur (Proc. Am. Phil. Soc. **64**: 177. 1925) under *P. levis*. Spegazzini (An. Mus. Nac. Buenos Aires **19**: 319. 1909) reported a rust on the same host under the name *Uredo rottboellii* but it may very well be *U. mira*.

Uredo morobeana Cummins, sp. nov. Urediis subepidermalibus, in maculis brunneis sparsis, plerumque hypophyllis, oblongis, 0.2–0.5 mm. longis, pulverulentis, brunneis, epidermide rupta conspicue; paraphysibus nullis; urediosporae globoideae vel late ellipsoideae, 20–27 × 25–32 μ; mem-

brana 1.5–2 μ cr., aureo- vel pallide cinnamomeo-brunnea, moderate echinulata; poris germ. 3 vel 4, aequatorialibus.

On *Eulalia* (*Pollinia*) *fulva*, NEW GUINEA: Morobe: Kajabit Mission Dec. 2, 1939, *Clemens 10857* (TYPE).

U. morobeana is nearer to *P. kimurai* Hirats. & Yosh., which I have been able to examine through the courtesy of Dr. Hiratsuka, than to other species which parasitize *Eulalia* or related genera, but the urediospores of *P. kimurai* average slightly smaller and are more deeply pigmented and more closely echinulate. The absence of paraphyses serves to separate *U. morobeana* from most species which occur on *Eulalia*.

Uredo eulaliae-fulvae Cummins, sp. nov. Urediis amphigenis, subepidermalibus, longitudinaliter tarde dehiscentibus, in maculis brunneis sparsis vel plus minusve striatis, oblongis vel linearis, 0.4–1.0 mm. longis, brunneis; paraphysibus brevibus, inconspicuis, obovoideis, 5–28 μ latis, 23–30 μ altis, membrana ubique 1 μ cr., hyalina; urediosporae obovoideae vel oblongae, (17–) 19–26 (–28) × 29–38 (–42) μ; membrana flavida vel aurea, 1.5 μ cr. vel ad apicem 2–4 μ cr., laxiuscule echinulata; poris germ. obscuris, verisimiliter 5, aequatorialibus.

On *Eulalia* (*Pollinia*) *fulva*, NEW GUINEA: Morobe: Kajabit Mission, Oct. 3, 1939, *Clemens 10719*, Dec. 13, 1939, *Clemens s.n.*; Wantoat, Jan. 13, 1940, *Clemens 10978* (TYPE); Matap station, Mar. 8, 1940, *Clemens s.n.*; Boana, May 15, 1940, *Clemens s.n.*

Mrs. Clemens' notes indicate that the uredia are golden when fresh, but they appear brownish when dry. The spores are pale golden or nearly hyaline, are frequently angular, and have an apical wall which may be uniform or slightly thickened. Hyaline, thin-walled structure which collapse easily and which I assume should be interpreted as paraphyses are present in the sori but are inconspicuous and easily overlooked.

U. eulaliae-fulvae differs from *U. morobeana* and from other rusts on *Eulalia* because of the large, pale spores and the peculiar paraphyses.

Uromyces nattrassii Cummins, sp. nov. Pycniis epiphyllis, subepidermalibus, paraphysatis, globoideis, 100–135 μ diam. Aecia pycnia circulariter circumdantia, amphigena vel caulicola, subepidermalia, in maculis moderate incrassatis usque ad 8 mm. diam., confluentibus, cinnamomea, pulverulenta, uredinoidibus; aeciosporae globoideae vel late ellipsoideae, 23–28 × 26–33 μ; membrana 2.5–3 μ cr., cinnamomea vel pallide castanea, moderata denseque verrucosa; poris germ. 2, aequatorialibus. Teliis aeciis conformibus sed pallide flavidis et compactis; teliosporae ovoideae vel oblongae, ad apiceum rotundatae vel plus minusve truncatae, deorsum attenuatae, (16–) 18–24 (–26) × (25–) 30–40 μ; membrana 1.5–2 μ cr., ad apicem 6–11 μ, hyalina vel pallide flavidula, levi, pedicello hyalino, persistenti, usque ad 90 μ longo; statim germ.

On *Statice spicatum*, CYPRUS: Famagusta, May 1935, *R. M. Nattrass 512* (TYPE).

Uromyces nattrassii differs from species described previously on related hosts in having colorless teliospores and uredinoid aecia. Apparently, uredia are not formed or, if formed, do not differ from the aecia. The aecia and telia occur in a more or less complete ring around the pycnia, the telia commonly developing in the aecia.

Nattrass (A first list of Cyprus fungi. 1937, p. 23) reported the above collection, together with two other specimens (Nos. 489, 490) on the same host and two specimens on *S. limonium*, as *Uromyces limonii* (DC.) Lév. The rust on *S. limonium* was probably as reported. Apparently, neither the pycnia nor the telia were detected on *S. spicatum*. Nattrass published notes, made by W. F. Steven of the Imperial Mycological Institute, pointing out that "No. 490 is similar in all respects, including malformation of the stems, to No. 3101, in Herb. Kew, on *Statice sinuata* L. from the Island of Lemnos, Greece (Exsicc. Mus. Hist. Pat. Vindobin 1925)." This may indicate that *U. nattrassii* also occurs on *S. sinuata* but an examination of the specimen would be necessary to decide the point, since Sydow (Monogr. Ured. **2**: 42. 1910) and Malençon (Rev. Mycol. **1**: 270. 1936) report *S. sinuata* under *U. limonii*. Malençon states that "les téleutosores sont rares" which would indicate that he saw telia. In referring, in the discussion following his description of *Uromyces statices-mucronatae*, to the rust on *S. sinuata* he writes (*l. c.*, p. 271) "—; d'autre part, sur *Statice sinuata*, ces urédosores forment de grosses pustules, nombreuses, généralement confluentes et déformantes, bordées par les tissus rougis de la plante."

Presumably, Nattrass' specimens Nos. 489 and 490 on *S. spicata* will be found to be *U. nattrassii* but this, as well as the identity of the rust on *S. sinuata*, can be decided only when the specimens have been compared with the above description.

UROMYCES PUSTULATUS Wakef. (fig. 8), on *Bauhinia fassoglensis*, KENYA: Kibos, Feb. 1921, *T. D. Maitland* (TYPE); UGANDA: Kiterera, Busoga, Sept. 1940, *C. G. Hansford 2811*.

The teliospores of this microcyclic species were originally described (Bull. Misc. Inform. Kew **1922**: 163) as verrucose but are actually finely reticulate. It is necessary to examine the spores soon after mounting since the outer portion of the wall swells and then usually appears to be verrucose. In the portion of the type received from Miss Wakefield the sori are on the pods while in Hansford's specimen they occur on the leaf blades, where they cause slight distortion, and on the petioles and stems.

U. pustulatus is near to *U. goyazensis* P. Henn., which has finer reticulations, a less pronounced apical thickening, and somewhat longer, narrower spores and to *U. floralis* Vestergr., which has about the same reticulation but a thinner apical wall. The only other African species with reticulate teliospores is *U. rhodesicus* Wakef. It has uredia in the life cycle, as does *U. congoensis* with verrucose teliospores, and the teliospores are globoid or depressed globoid and dark brown and opaque.

THE ARTHUR HERBARIUM, PURDUE UNIVERSITY AGRICULTURAL
EXPERIMENT STATION
LAFAYETTE, INDIANA

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 5, pp. 531-532 SEPTEMBER, 1943

A NEW SPECIES OF SPHAERALCEA FROM NEW MEXICO[1]

C. L. PORTER

Sphaeralcea procera Porter, sp. nov. Planta perennis, molliter lignosa, incana, fere 3 m. alta, ramis adscendentibus numerosis. Caulis pili fere 0.5 mm. longi, radiis fere 16. Lamina foliorum 1–5 cm. longa, coriacea, infra prominenter venosa, rugosa, marginibus crispis, ovato-oblonga, ad basim cuneata ad apicem acuta vel obtusa, 3 venis validis a base provenientibus, plerumque 3-lobata, lobo terminali quam lobo lateriore largiore, margine irregulariter dentata. Petiolus 5–10 mm. longus. Inflorescentia angusta, densa, interrupta, thyrsoidea, fere usque ad apicem foliacea. Pedicelli calyci breviores. Calyx ad faciem dorsalem dense pubescens, fere 5 mm. altus, lobis deltoidis tubum aequantibus vel pauce excedentibus. Corolla roseo-purpurea. Carpelli fere 10, fere 3 mm. alti et 2 mm. lati, galeatiformes, crasso-reticulati. Ovuli 2 et semina 1 in quoque carpello, seminis margine pubescenti.

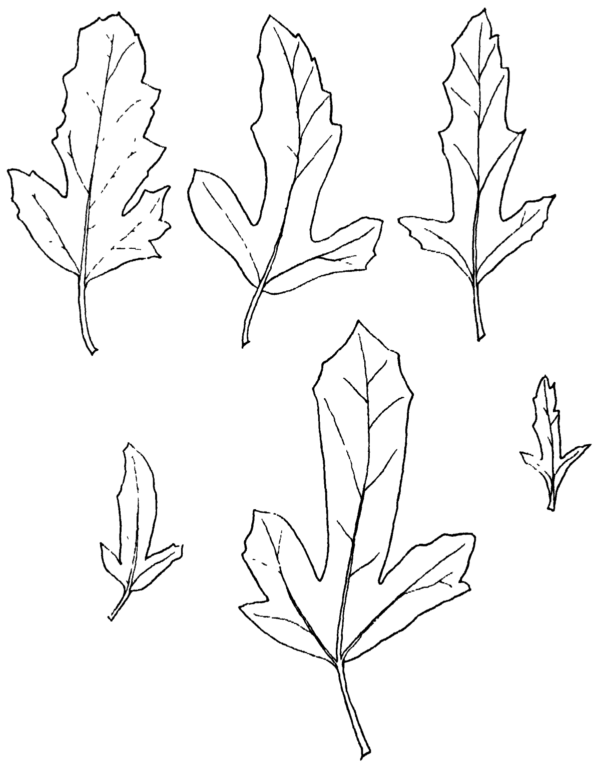


FIG. 1. *Sphaeralcea procera*; representative leaves from the type. × 1.

[1] Contributions from the Department of Botany and the Rocky Mountain Herbarium of the University of Wyoming No. 195.

TYPE: *C. L. Porter 3037*, collected in a dry sandy arroyo about 20 miles north-east of Deming, Luna County, New Mexico, September 14, 1941, in the Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming. Isotypes in the herbaria of the Missouri Botanical Garden and the New York Botanical Garden, and in the U. S. National Herbarium.

This species may be referred to the subgenus *Eusphaeralcea* and the section *Emoryanae*. It is immediately distinguished from all species in the United States by its size and shrubby nature and from the species in its section by the nature of the carpels. In leaf characters it approaches *S. emoryi variabilis* (Cockerell) Kearney, to which it might be considered as most closely allied.

FIG. 2. *Sphaeralcea procera*; a single carpel from the type. × 15.

The species described above was encountered while the writer was on a botanical collecting trip in the Southwest which was financed partly by a Grant-in-Aid from the Sigma Xi Alumni Research Fund, and it is a pleasure to acknowledge the assistance thus obtained.

THE ROCKY MOUNTAIN HERBARIUM, UNIVERSITY OF WYOMING
LARAMIE, WYOMING

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 5, pp. 533–549 SEPTEMBER, 1943

STUDIES ON PACIFIC ISLAND PLANTS—III NEW AND NOTEWORTHY FLOWERING PLANTS FROM FIJI

A. C. SMITH

The species discussed in the following pages are either novelties, or represent range-extensions into Fiji, or are sufficiently unusual to merit notes. The greater part of the herbarium material which is the basis of this study was forwarded from the Bernice P. Bishop Museum in 1941, and I am indebted to the authorities of that institution, and especially to Miss Marie Neal, for their cooperation. The place of deposit of cited specimens is indicated by the following parenthetical abbreviations: Arnold Arboretum (A), Bishop Museum (Bish), Gray Herbarium (GH).

Two families here mentioned, Alismaceae and Iridaceae, have not otherwise been recorded from Fiji; both are represented by introduced species. The genera *Scirpodendron* and *Rhamnella*, represented by species native to the group, are here first reported from Fiji, while the following genera are apparently first listed from the group and are based upon records of introduced species: *Sagittaria*, *Sisyrinchium*, *Tritonia*, *Hedychium*, *Senebiera*, *Gynandropsis*, *Samanea*, and *Albizzia*.[1] In this treatment ten species are described as new and two new combinations are proposed.

TAXACEAE

DACRYDIUM LYCOPODIOIDES Brongn. & Gris in Bull. Soc. Bot. Fr. **16**: 329. 1869; A. C. Sm. in Bishop Mus. Bull. **141**: 11. 1936.

VITI LEVU: Naitasiri: Central Road, 8 miles from Suva, alt. 240 m., *MacDaniels 1151* (Bish) (tree 35 m. high, the trunk 120 cm. diam.; timber good; in rain-forest).

Previously recorded, in Fiji, only from a single collection from Vanua Levu.

ALISMACEAE

SAGITTARIA SAGITTIFOLIA L. Sp. Pl. 993. 1753.

VITI LEVU: Naitasiri: Rewa Delta, in water along Wainimbokasa River, *MacDaniels 1020* (Bish).

This widespread species, perhaps a recent introduction into Fiji, has been reported in the Pacific area only from Hawaii and Raratonga. Our specimen represents a broad-leaved form.

[1] In a recent paper entitled "The adventive and weed flora of the leeward coasts of Fiji," in Proc. Linn. Soc. **154**: 92–106. 1943, William Greenwood has listed a few species which are discussed as new records in the present paper, which was prepared before the cited publication was available.

TRIURIDACEAE

ANDRURIS VITIENSIS (A. C. Sm.) Giesen in Pflanzenr. 104 (IV. **18**): 28. 1938; A. C. Sm. in Sargentia **1**: 5. 1942.

VITI LEVU: Naitasiri: Korombamba Mt., woods near summit, alt. 550 m., *Gillespie 2352* (Bish).

This species has previously been reported only from Vanua Mbalavu and Vanua Levu.

GRAMINEAE

(determinations by Agnes Chase)

ISCHAEMUM TIMORENSE Kunth, Rév. Gram. **1**: 369. *pl. 98.* 1830; Lauterb. in Bot. Jahrb. **41**: 222. 1908.

VITI LEVU: Rewa: Between Navua and Suva, *Greenwood 817* (GH) (in clumps up to 60 m. high).

This species has apparently not previously been recorded from Fiji and is known from the nearby groups only from Lauterbach's mention of it in Samoa.

PASPALUM DISTICHUM L. Amoen. Acad. **5**: 391. 1759, Syst. Nat. ed. 10. **2**: 855. 1759; Rechinger in Denkschr. Akad. Wiss. Wien **81**: 301. 1907; Christoph. in Bishop Mus. Bull. **128**: 10. 1935.

VITI LEVU: Lautoka: Lautoka, *Greenwood 830* (GH) (creeping perennial, up to 30 cm. high, on dry hillsides).

Although reported from Samoa and other Pacific groups, this species appears not to have been previously listed from Fiji.

ERAGROSTIS UNIOLOIDES (Retz.) Nees ex Steud. Pl. Glum. **1**: 264. 1854.

VITI LEVU: Nandronga: Singatoka, *Greenwood 815A* (GH) (on dry hills at roadside).

Apparently this plant has not otherwise been reported from Fiji or any of the nearby groups. Mr. Greenwood states that it was first seen in Fiji at Navua (Viti Levu) in 1939, since which time it has evidently spread along the road to Lautoka; only a few patches were seen at the cited locality.

CYPERACEAE

SCIRPODENDRON GHAERI (Gaertn.) Merr. in Philip. Jour. Sci. Bot. **9**: 268. 1914. *Chionanthus Ghaeri* Gaertn. Fruct. **1**: 190. *t. 39, f. a–e.* 1788. *Ptychocaryum Ghaeri* H. Pfeiff. in Rep. Sp. Nov. **21**: 240. 1925, **28**: 20. 1930.

VITI LEVU: Serua: Thulanuku, near Ngaloa, *Degener 15103* (GH) (in marsh near ocean; native name: *misimisi*). VANUA LEVU: Thakaundrove: Maravu, near Salt Lake, *Degener & Ordonez 14249* (GH) (herb up to 1 m. high, in marsh in coconut plantation near sea; leaves used for thatching).

This species has not otherwise been reported from Fiji, although it is known from Samoa, usually having been reported under the synonym of *Scirpodendron costatum* (Thw.) Kurz; it is also recorded from Micronesia. We also have available a collection from the New Hebrides (Santa Cruz Group: Vanikoro: *Kajewski 662* [GH], in salt-water swamp in rain-forest, with leaves up to 2.5 m. long).

Pfeiffer, in the publications cited above, has referred this plant to *Ptychocaryum* R. Br., apparently believing that this genus was validly published before *Scirpodendron* Zippel ex Kurz (1869). I am unable to find that this

is the case. The name *Ptychocarya* (not *Ptychocaryum*) apparently first appears in Wallich's Catalogue (p. 123, no. 3538. 1830) under *Scleria macrocarpa* Wall., as "*Ptychocarya*, illustr. R. Br. (gen. nov.)." The combination *Ptychocarya macrocarpa* seems to have been first made by Steudel (Nomencl. ed. 2. **2**: 416. 1841), without comment. Lindley (Veg. Kingd. 119. 1846) lists *Ptychocarya* R. Br. without description or reference to an earlier description.

It thus appears that *Ptychocarya* was not adequately published before 1869 and that it cannot be taken to replace *Scirpodendron*. The spelling of Brown's name was "corrected" by Post and Kuntze (Lexic. 470. 1904) to *Ptychocaryum*, which was adopted by Pfeiffer. The more complete synonymy of the species was given by Pfeiffer in 1930. I am indebted to Dr. H. W. Rickett for verifying the above conclusions as to the proper binomial for this plant.

IRIDACEAE

Sisyrinchium micranthum Cav. Dissert. Bot. (6). 345. *pl. 191, f. 2.* 1788.

Viti Levu: Tholo North: Vicinity of Nandarivatu, in pastures, alt. 900 m., *Gillespie 3728* (Bish, GH) (native name: *ua ma ndrali*).

This American plant has become widely distributed; in the Pacific it has been reported from Easter Island and New Caledonia, and it is naturalized in southeastern China. It was doubtless accidentally introduced into Fiji. The genus has not otherwise been reported from the group, nor, as far I can ascertain, has any representative of the family Iridaceae.

Tritonia crocosmiaeflora (Lem.) Nichols. Dict. Gard. **4**: 94, as *T. crocosmiflora*. 1887. *Montbretia crocosmiaeflora* Lem. ex André in Rev. Hort. **54**: 124. *pl.* 1882.

Viti Levu: Tholo North: Nandarivatu, in open waste places, alt. 1000 m., *Parks 20658* (Bish).

This common garden hybrid has apparently escaped from cultivation and should be listed among the adventive plants of Fiji. It has been reported as naturalized in Hawaii by Degener (Pl. Haw. Nat. Park 105. *pl. 25.* 1930).

ZINGIBERACEAE

Hedychium coronarium Koenig in Retz. Obs. Bot. **3**: 73 1783; K. Schum. in Pflanzenr. 20 (IV. **46**): 44. 1904.

Fiji, without definite locality: *Gillespie, 1391* (Bish, fls. only) (flowers white, fragrant, worn in hair by dancers; native name: *the vunga*).

This widely cultivated species is commonly found in Fijian villages and is probably more or less naturalized, but it appears not to have been previously recorded from the group.

ULMACEAE

Celtis Harperi Horne ex Baker in Jour. Linn. Soc. Bot. **20**: 371. 1883.

Vanua Levu: Mbua: Southern portion of Seatovo Range, alt. 100–350 m., *Smith 1568* (GH) (slender tree 4 m. high, in forest); Thakaundrove: Natewa Peninsula, Uluingala, alt. 600–820 m., *Smith 1976* (GH) (tree 8 m. high, in dense forest).

The only species of *Celtis* thus far reported from Fiji is *C. Harperi*, based on a specimen collected by Horne between Wai Wai and Lomaloma, Vanua

Levu. The original description of this species, although brief, indicates that *C. Harperi* is represented by the two specimens cited above, rather than by the Viti Levu specimens cited in connection with the following species. Baker's mention of the leaf-blades as 3–4 inches long, 1½ inches broad, and acute seems to exclude the Viti Levu specimens, which have the blades smaller and obtuse.

The Vanua Levu specimens here cited have the petioles 10–20 mm. long, the leaf-blades 8–13.5 cm. long and 4–6 cm. broad (about 3–5¼ by 1½–2¼ inches), obtusely cuspidate or short-acuminate, usually callose-mucronulate at apex, and conspicuously 3-nerved from the base, with 2–4 pairs of weak secondaries arising from the costa. The fruiting inflorescences are up to 7 cm. long, 2 or 3 times dichotomously branched, or reduced and essentially simple; the drupes are ovoid, up to 12 mm. long and 8 mm. broad, and abruptly narrowed to the persistent stigmas.

On the basis of many modern interpretations of *C. paniculata* (Endl.) Planch., one might take *C. Harperi* to be a synonym, but I am inclined to doubt that *C. paniculata* has the extensive Pacific range accredited to it by F. Brown (in Bishop Mus. Bull. **130**: 29–32. 1935) and others. It may also be questioned whether the plant mentioned as *C. paniculata* by Kanehira (Fl. Micron. 82. *f. 11.* 1933) and other workers on Micronesia is the same as the Norfolk Island plant which was the basis of Planchon's combination (*Solenostigma paniculatum* Endl. Prodr. Fl. Norfolk. 42. 1833). On the basis of the original description, Australian herbarium specimens, and the interpretations of students of the Australasian flora (e.g., Banks and Soland. Ill. Austr. Pl. [Bot. Cook's Voy.] **3**: 90. *pl. 298.* 1905), one observes that the leaves of *C. paniculata* have comparatively short petioles, inconspicuous lateral basal nerves which are scarcely stronger than the several upper secondaries, and a gradually acuminate apex.

Celtis vitiensis A. C. Sm., sp. nov.

Arbor ad 4 m. alta (vel ultra?) sub fructu ubique glabra, ramulis gracilibus subteretibus cinereis copiose lenticellatis; stipulis subcoriaceis acutis 2–4 mm. longis demum caducis; petiolis gracilibus leviter canaliculatis 4–10 mm. longis; laminis chartaceis in sicco fusco-olivaceis utrinque papillato-rugulosis, ellipticis vel ovato-ellipticis, (3–) 4–9 cm. longis, (1.5–) 2–4 (–4.5) cm. latis, basi obtusis et in petiolum saepe inaequilateraliter decurrentibus, apice late obtusis vel subrotundatis et saepe inconspicue emarginatis, margine integris et leviter recurvatis, e basi trinerviis, costa supra paullo elevata subtus prominente, nervis primariis 2 supra medium laminae arcuatim productis exterius venas paucas inconspicuas emittentibus, nervis secundariis utrinsecus 2 vel 3 inconspicuis plerumque utrinque prominulis, rete venularum immerso vel interdum subtus prominulo; cymis fructiferis 1–2 cm. longis pauciramosis, pedicellis 1–3 mm. longis; drupis elongato-ovoideis, maturitate 8–9 mm. longis et 5–6 mm. latis, inconspicue 2-angulatis, basi obtusis vel rotundatis, apicem versus abrupte angustatis, stigmatibus conspicue bilobatis complanatis subpersistentibus.

VITI LEVU: Tholo North: Vicinity of Nandarivatu, alt. 750 m., *Degener 14322* (A—TYPE), Feb. 9, 1941 (tree 4 m. high, on forested stream-bank; fruit blue-black, succulent); Nandrau, alt. about 600 m., *Degener 14897* (A) (in forest); trail around escarpment behind Government Station, Nandarivatu, alt. 800 m., *Gillespie 4185* (Bish, GH).

Similarly a member of the Subgenus *Solenostigma* (Endl.) Planch., *C. vitiensis* differs from *C. Harperi* Horne, doubtless its closest ally, in its shorter petioles, smaller leaf-blades with papillate-rugulose surfaces and obtuse or nearly rounded apices, and smaller drupes. The cited specimens were originally distributed to various herbaria under the name of *C. Harperi*. Degener reports the native names of *marasa* and *matho* for his nos. *14322* and *14897* respectively, but these names usually refer to species of Sapindaceae and Lauraceae.

PROTEACEAE

KERMADECIA FERRUGINEA A. C. Sm. in Bishop Mus. Bull. **141**: 48 1936.

TAVEUNI: Trail above Somosomo, alt. 1000 m., *Gillespie 1842* (A, Bish) (on exposed summit ridge; native name: *kau mbutu*). WITHOUT DEFINITE LOCALITY: ["other side of W."], *Gillespie 3201* (A, Bish) (native name: *thivea*).

Of the above-cited collections, the first was obtained near the type locality, and it is quite probable that Gillespie's cryptic locality for his no. *3201* refers to Waiyevo, one of his other stations on Taveuni. Each of the cited collections is accompanied by a detached fruit and has leaves larger and older than those originally described, making desirable the following amplification of the description:

Petioles up to 6.5 cm. long; leaf-blades up to 17 cm. long and 12.5 cm. broad, subcordate to inequilaterally subacute at base, often nearly rounded at apex, lightly undulate and essentially entire at margins, persistently ferruginous-tomentose on the main nerves above or glabrescent, at length nearly glabrescent beneath, the principal secondary nerves often 4 or 5 pairs; raceme up to 9 cm. long in fruit; fruit coriaceous when dried, ellipsoid or ovoid, slightly flattened, at maturity up to 23 mm long, 20 mm. broad, and 14 mm. thick, rounded at base, subacute and perhaps mucronulate at apex, the pericarp probably carnose when fresh, blackish when dried.

PORTULACACEAE

TALINUM PANICULATUM (Jacq.) Gaertn. Fruct. **2**: 219. *pl. 128*. 1791; v. Poelln. in Rep. Sp. Nov. **35**: 10. 1934.

OVALAU: Along coastal road north of Levuka, near sea, *Gillespie 4195* (Bish, GH).

This widespread weed has already been reported from Fiji, under the synonym *T. patens* (L.) Willd., by Seemann (Fl. Vit. 10. 1865). It is thus far recorded, in Fiji, only from Ovalau, but apparently it is common in the Society Islands. A native of tropical America, the species is now widely naturalized in China.

DEGENERIACEAE

DEGENERIA VITIENSIS I. W. Bailey & A. C. Sm. in Jour. Arnold Arb. **23**: 357. *pl. 1–5*. 1942.

VITI LEVU: Naitasiri: Nanduna, alt. about 90 m., *B. E. Parham 1488* (A) (tree about 18 m. high, in forest; native name: *masiratu;* timber useful).

The recently described monotypic Degeneriaceae has previously been known only from collections in Tholo North, Viti Levu, and Mbua, Vanua Levu. The third collection, cited above, comes from the southeastern portion of Viti Levu; its foliage precisely matches that of the type and it is ac-

companied by an old fruit which offers no characters not brought out in the original description. Mr. Parham states that the species is fairly frequent in the cited region.

ANNONACEAE

Polyalthia angustifolia A. C. Sm., sp. nov.

Arbor sub fructu ubique glabra; ramulis gracilibus subteretibus rugulosis inconspicue lenticellatis; petiolis canaliculatis 6–10 mm. longis superne anguste alatis; laminis subcoriaceis in sicco fuscis oblongo-lanceolatis, (6–) 12–17.5 cm. longis, (2.5–) 3–4 cm. latis, basi subacutis et in petiolum inconspicue decurrentibus, apice obtusis vel breviter et obtuse cuspidatis, margine integris et leviter recurvatis, costa supra valde impressa subtus prominente, nervis secundariis utrinsecus 7–12 brevibus arcuatis anastomosantibus supra subplanis subtus prominulis, rete venularum immerso vel subtus paullo prominulo; infructescentiis ut videtur breviter pedicellatis, pedicello sub fructu crasso tereti ruguloso 2 cm. vel ultra longo, lobis calycis persistentibus 3 subcoriaceis late deltoideis ad 2 mm. longis obtusis; receptaculo subgloboso sub fructu ad 7 mm. diametro; carpellis maturis ut videtur circiter 12 breviter stipitatis (stipitibus crassis ad 2 mm. longis) obovoideo-ellipsoideis, 15–22 mm. longis, 12–15 mm. latis, apice rotundatis, pericarpio coriaceo tenui inconspicue ruguloso; seminibus 1 vel 2 adscendentibus obovoideis vel subglobosis, ad 14 mm. longis et 11 mm. latis, interdum subcomplanatis et leviter carinatis.

VITI LEVU: Naitasiri: Tamavua woods, 7 miles from Suva, alt. 150 m., *Gillespie 2198* (A—TYPE, Bish, GH), Aug. 9, 1927.

Polyalthia angustifolia is readily distinguished from the other Fijian species of the genus by its long narrow leaf-blades with subacute bases. The carpels, with one or two erect seeds, indicate the probable place of the new species in *Polyalthia*, but this position should be verified by the collection of flowers.

Xylopia pacifica A. C. Sm., sp. nov.

Arbor ubique praeter inflorescentiam demum subglabra vel ramulis apicem versus et petiolis cinereo-puberula; ramulis gracilibus teretibus cinereis copiose lenticellatis; petiolis rugulosis canaliculatis 2–6 mm. longis, superne basi laminae decurrente alatis; laminis subcoriaceis siccitate fuscis ovatis vel ellipticis, 4.5–11 cm. longis, 2.5–5 cm. latis, basi obtusis et in petiolum abrupte decurrentibus, apice cuspidatis vel acuminatis (acumine ipso ad 8 mm. longo obtuso), margine integris, subtus pilis ad 0.5 mm. longis cinereo-hirtellis demum glabrescentibus, supra costa interdum breviter pilosa excepta glabris, costa conspicua utrinque prominente, nervis secondariis utrinsecus 7–18 cum aliis debilioribus interspersis patentibus utrinque valde prominulis marginem versus anastomosantibus, rete venularum copiosarum intricato utrinque prominulo; inflorescentiis axillaribus vel e ramulis infra folia orientibus brevibus 1- vel 2-floris, rhachi pedicellisque primo dense sericeo-puberulis, rhachi 2–3 mm. longa, bracteis mox caducis; pedicellis crassis 2.5–3 mm. longis basim versus 1 mm. superne ad 2 mm. diametro; calyce ut pedicello puberulo coriaceo late cupuliformi, sub anthesi 3–4 mm. longo et circiter 6 mm. diametro, intus glabro, sepalis 3 late ovato-deltoideis, circiter 2 mm. longis, 4–5 mm. latis, apice obtusis vel rotundatis; corolla cylindrico-urceolata inconspicue hexagona, basi dilatata,

immatura ad 9 mm. longa, petalis 6 carnosis valvatis biseriatis, exterioribus 3 lanceolatis basim versus circiter 5 mm. latis, extus dense pallido-sericeis, intus copiose pallido-puberulis, interioribus 3 brevioribus dense puberulis e basi incrassata circiter 2.5 mm. lata subulatis; toro subconico circiter 1 mm. alto externe staminifero medio profunde excavato apice irregulari; staminibus circiter 200 arcte imbricatis 1.3-1.5 mm. longis, filamentis ligulatis 0.2–0.5 mm. longis, connectivo in appendiculam minutam complanatam obscure papillosam producto, loculis linearibus obscure septatis; pistillis circiter 5 cavitate tori inclusis oblongo-ellipsoideis, stylo brevi incluso circiter 1.4 mm. longis, pilis 0.3–0.5 mm. longis apice excepto copiose pallido-sericeis, ovulis ut videtur circiter 12 oblique superpositis; pedicellis sub fructu crassis teretibus rugosis ad 15 mm. longis, receptaculo demum valde incrassato; carpellis maturis 2–4 inaequilateraliter ellipsoideis vel obovoideo-ellipsoideis, 25–32 mm. longis (stipite crasso circiter 4 mm. longo et 4–6 mm. diametro excepto), 16–21 mm. latis et crassis, inconspicue longitudinaliter carinatis, apice rotundatis, pericarpio fibroso-lignoso 1-1.5 mm. crasso inconspicue papilloso-ruguloso vel sublevi, primo nigrescente demum cinereo-variegato, seminibus 8–12 (vel in fructibus minoribus 3 vel 4), eis basim et apicem versus parvis, eis medium versus inaequilateraliter obovoideo-ellipsoideis conspicue complanatis, circiter 16 mm. longis et 10 mm. latis, 4–5 mm. crassis, basi et apice obtusis.

VITI LEVU: Tholo North: Nandarivatu, alt. 900 m., *Gillespie 4153* (A, Bish, GH), *4313* (Bish); Rewa: Lami, alt. 100 m., *Parks 20912* (Bish) (tree 6 m. high; trunk 8 cm. diam.; in thick forest); Naitasiri: Tholo-i-Suva, alt. about 180 m., *B. E. Parham 2651* (A– TYPE), Jan. 16, 1939 (tree 8 m. high, in forest), Nasinu, 9–10 miles from Suva, alt. 150 m., *Gillespie 3483* (A, Bish, GH), *3615* (A, Bish, GH) (in woods west of road), *3663* (A, Bish, GH) (large tree; trunk 20 cm diam.; fruit dark green).

Xylopia pacifica, the third species of the genus known from Fiji, in vegetative characters strongly suggests the two already known, differing from them in its much shorter petioles, its leaf-blades with more obviously decurrent bases and somewhat less prominent venation, and its different torus, which is irregular at the distal margin and forms a deeper carpellary cavity. The stamens of the new species are very numerous, being larger than those of *X. vitiensis* A. C. Sm. and smaller than those of *X. Degeneri* A. C. Sm.

Of the cited specimens, only the type bears flowers, and this collection is accompanied by a single detached mature carpel. The remaining specimens are in fruit. The type and *Gillespie 3483* are identical in foliage, differing from the remaining specimens in having leaves with longer acumens and slightly less obvious venation. There is also considerable variation in the fruits of the cited specimens. Those described above are of the most mature carpels, as found on the type and *Gillespie 3483*. The remaining specimens have carpels only 13–18 by 10–16 mm. with comparatively slender stipes about 2 mm. thick; the pericarp of these carpels is 0.7-1 mm. thick, and the seeds are 3 or 4 in number and only 6–10 mm. long and broad. The difference in number of seeds does not seem consequential, as carpels associated with *Gillespie 3483* may have as few as 4 or as many as 10 seeds. Twelve seeds were observed only in the single fruiting carpel of the Parham specimen. The differences here pointed out among the available specimens seem no more than individual, and I confidently refer the material to a single species.

MYRISTICACEAE

MYRISTICA MACRANTHA A. C. Sm. in Bishop Mus. Bull. **141**: 67. *f. 33.* 1936, in Bull. Torrey Bot. Club **68**: 399. 1941.

VITI LEVU: Naitasiri: Mt. Korombamba, alt. 300–400 m., in dense forest on upper slopes, *Parks 20123* (Bish).

This species has previously been known only from two collections from Vanua Levu.

CRUCIFERAE

SENEBIERA DIDYMA (L.) Pers. Syn. Pl. **2**: 185. 1806.

VITI LEVU: Tholo North: Nandarivatu, alt. about 800 m., *Greenwood 880* (GH) (semiprostrate in waste places).

Although this widespread weed has been reported from other Pacific groups, including Tonga, I believe that it has not otherwise been recorded from Fiji.

CAPPARIDACEAE

GYNANDROPSIS SPECIOSA (H. B. K.) DC. Prodr. **1**: 238. 1824.

FIJI, WITHOUT DEFINITE LOCALITY: *Gillespie 2821* (Bish, GH) (flowers dull rose-pink).

This tropical American plant, although now known in many parts of the Old World tropics as a weed, has apparently not been reported from Fiji or the adjacent regions. The genus is also new to Fiji.

LEGUMINOSAE

SAMANEA SAMAN (Jacq.) Merr. in Jour. Wash. Acad. Sci. **6**: 47. 1916.

VITI LEVU: Tholo North: Vicinity of Nandarivatu, alt. 700 m., *Gillespie 4378* (Bish).

The widely cultivated rain-tree, a native of northern South America, has been reported from several Pacific groups, but as far as I know it has previously escaped notice in the literature pertaining to Fiji.

ALBIZZIA LEBBECK (L.) Benth. in Hook. Lond. Jour. Bot. **3**: 87. 1844.

VITI LEVU: Rewa: Along the coast between Suva and Lami, *Gillespie 2064* (A, Bish).

This widely cultivated plant has not been previously reported from Fiji, although records of it from many other Pacific groups are found in literature. It is probably a native of the drier parts of Africa and Asia. The genus has not otherwise been recorded from Fiji.

ACACIA FARNESIANA (L.) Willd. Sp. Pl. **4**: 1083. 1805.

VITI LEVU: Ra: Ellington, on strand, *Parks 20856* (Bish) (tree 4 m. high).

This species, well established in most tropical countries and probably a native of America, has not previously been reported from Fiji in taxonomic literature. Its occurrence has been noted in most of the major Pacific groups.

MIMOSA INVISA Mart. in Flora **20**: Beibl. 121. 1837.

Schrankia distachya "vel aff." sensu A. C. Sm. in Sargentia **1**: 36. 1942; non DC.

Mr. William Greenwood calls my attention to the fact that the sterile specimen (*Greenwood 838*) which I referred tentatively to *Schrankia distachya* in 1942 actually represents *Mimosa invisa*. This latter species has been reported from Fiji by Mr. B. E. V. Parham in the Agricultural Journal of the Department of Agriculture, Fiji, in a recent number which is not yet available to me. Apparently seeds of this weed were accidentally introduced into Fiji from Malaysia, where the Brazilian plant has been established for some time; it has not been reported otherwise from the Pacific. Mr. Parham reports it from Singatoka and Tailevu on Viti Levu. The genus *Schrankia* is therefore not known from Fiji.

BAUHINIA MONANDRA Kurz in Jour. As. Soc. Beng. **42**(2): 73. 1873.

FIJI, WITHOUT DEFINITE LOCALITY: *Gillespie 4399* (A, Bish).

Although reported from various other Pacific regions, this species, probably a native of tropical America, is apparently here listed from Fiji for the first time.

PUERARIA THUNBERGIANA (Sieb. & Zucc.) Benth. in Jour. Linn. Soc. Bot. **9**: 122. 1867; A. C. Sm. in Sargentia **1**: 39. 1942. *Pachyrhizus trilobus* sensu Seem. Fl. Vit. 63. 1865; Horne, A Year in Fiji 265. 1881; Guppy, Obs. Nat. Pac. **2**: 412, 413. 1906; Gibbs in Jour. Linn. Soc. **39**: 209. 1909; non DC. *Pachyrhizus angulatus* sensu Horne, A Year in Fiji 86. 1881; non Rich.

TAVEUNI: *Gillespie 4702* (Bish); vicinity of Waiyevo, alt. 100 m., *Gillespie 4703* (A, Bish) (fls. violet). WITHOUT DEFINITE LOCALITY: *Seemann 114* (GH), *Horne 463* (GH).

I am indebted to Mr. William Greenwood, of Lautoka, for pointing out to me that Seemann had misidentified his plant (no. *114*) and had been followed in this determination by Horne, Guppy, and Gibbs. The cited notes of these writers refer to *Pueraria Thunbergiana*, as does the well known Fijian name *yaka*. This species was doubtless an early introduction into Fiji and may still be used as an emergency food plant.

The genus *Pachyrhizus* should therefore be excluded from lists of the Fijian flora. For notes on the identity of *Pachyrhizus trilobus* (Lour.) DC. [= *Pueraria Thomsoni* Benth.], see Merrill (Comm. Lour. Fl. Cochinch. 211. 1935) and Rehder (in Jour. Arnold Arb. **18**: 209. 1937). It is probable that certain other references to the occurrence of *Pachyrhizus* in the Pacific area will also be found to pertain to *Pueraria Thunbergiana*.

MELIACEAE

Aglaia Parksii A. C. Sm., sp. nov.

Arbor ad 5 m. alta, ramulis teretibus apicem versus ad 7 mm. crassis juventute densissime ferrugineo-tomentosis (pilis stellatis multiramulosis, ramulis nonnullis ad 1 mm. longis reliquis brevioribus demum descitis, pelta persistente et ut videtur multiciliata); foliis pinnatis ad 70 cm. longis, petiolis 14–18 cm. longis basi valde incrassatis et rhachi subteretibus ut ramulis dense tomentosis; foliolis 9 oppositis vel suboppositis, petiolulis tomentosis, lateralibus 6–13 mm. longis, laminis papyraceo-chartaceis oblongis (vel inferioribus subellipticis), 10–25 cm. longis, 5.5–8 cm. latis, basi anguste vel late rotundatis et subcordatis interdum inaequalibus, apice obtusis, margine integris et undulato-recurvatis, supra glabris vel costa parce tomentosis, obscure impresso-glandulosis, subtus costa pilis ut eis ramulorum

tomentosis ceterum glabris, costa supra leviter canaliculata vel subplana subtus prominente, nervis secundariis utrinsecus 12–19 (–25) patentibus marginem versus anastomosantibus supra subplanis subtus leviter elevatis, rete venularum utrinque subplano vel supra insculpto subtus leviter prominulo; inflorescentiis axillaribus racemosis vel forsan anguste paniculatis post anthesin 3–4.5 cm. longis paucifloris ubique dense stellato-tomentellis, pedunculo brevi vel subnullo et rhachi gracilibus, bracteis minutis mox deciduis; pedicellis 1.5–3 mm. longis sub calyce obscure articulatis; calyce cupuliformi paullo post anthesin circiter 2 mm. longo et 3 mm. summo diametro, lobis deltoideis, 0.5–0.7 mm. longis, circiter 1 mm. latis, acutis, intus glabris; petalis staminibusque non visis; ovario subgloboso dense et minute tomentello; fructibus immaturis ellipsoideis persistenter tomentellis.

VITI LEVU: Naitasiri: Tholo-i-Suva, alt. 200 m., *Parks 20076* (A—fragm., Bish—TYPE), May 24, 1927 (tree 5 m. high, the trunk 6 cm. diam.; in thick bush in a wet canyon).

Although the stamens of this species are not available, it may safely be referred to the Section *Hearnia* because of its obvious affinity to *A. Archboldiana* A. C. Sm., doubtless its closest ally. *Aglaia Parksii* differs from this, however, in its more numerous and more definitely oblong leaflets, of which the base is usually subcordate and the apex obtuse. The new species has a sparser and shorter tomentum throughout, and this is lacking from the lower surface of leaflet-blades, whereas in *A. Archboldiana* the blades are persistently tomentose beneath. The inflorescence of the new species is comparatively reduced and the calyx-lobes are much smaller. Another relative of *A. Parksii* is the common *A. vitiensis* A. C. Sm., which differs in its lepidote rather than tomentose indument, its differently shaped leaflets, its ample paniculate inflorescence, etc.

HIPPOCRATEACEAE

SALACIA PACHYCARPA A. C. Sm. in Sargentia **1**: 53. 1942.

VITI LEVU: Rewa: Near quarry west of Lami village, alt. 15 m., *Gillespie 4581* (A, Bish) (bush, on limestone rocks; fruit green).

This is the second collection of the species, the type having come from northeastern Viti Levu. Like the type, the Gillespie specimen is in fruit.

SAPINDACEAE

ALLOPHYLUS SUBLAXUS Gillespie in Bishop Mus. Bull. **83**: 16. *f. 18.* 1931.

VITI LEVU: Tholo North: Nauwanga, near Nandarivatu, alt. about 750 m., *Degener 14530* (A) (tree, in dense forest). TAVEUNI: Vicinity of Waiyevo, alt. 200–650 m., *Gillespie 4731, 4789* (Bish, GH) (on bank of stream or in stream-bed in woods above coconut plantations).

The cited specimens should be added to those originally listed by Gillespie from Viti Levu and Ovalau. In the specimens available to me the leaflet-apex varies from obtuse to short-acuminate, but in essential details there are no differences. All eight stamens appear to be fertile in the flowers I have examined, Gillespie's mention of "fertile anthers apparently 2" and his illustration having been based on an injured flower. The species is closely allied to *A. ternatus* (J. R. & G. Forst.) Radlk., being distinguished primarily by its compound inflorescences. The occurrence of *A. ternatus* east of the New Hebrides and New Caledonia is dubious.

Allophylus sublaxus differs from *A. vitiensis* Radlk. (recorded only from the type collection, *Horne 464* [GH], without definite locality) not only in the foliage character mentioned by Gillespie, but also in having its petals obovate and gradually narrowed toward the base rather than spatulate and with an obviously ligulate basal portion.

Allophylus umbrinus A. C. Sm., sp. nov.

Arbor parva, ramulis gracilibus teretibus juventute pilis 0.3–1 mm. longis dense tomentosis demum glabratis cinereis; foliis trifoliolatis, petiolo ut ramulis densissime tomentoso 6–9 cm. longo, petiolulis tomentosis lateralibus 1–4 mm. terminali ad 10 mm. longis, foliolorum laminis papyraceis in sicco olivaceis oblongo-ellipticis (lateralibus inaequilateralibus), 11–14 cm. longis, 5–7.5 cm. latis, basi acutis vel obtusis, apice obtuse cuspidatis et mucronulatis, margine remote mucronulato-serratis, utrinque praecipue subtus nervis densissime velutinis (pilis circiter 0.8 mm. longis) supra praeter nervos demum subglabratis, costa subtus prominente, nervis secundariis utrinsecus 8–10 rectis erecto-patentibus supra paullo subtus valde prominulis, rete venularum utrinque leviter prominulo; inflorescentiis paniculatis ad 9 cm. longis, rhachi et ramulis paucis ad 6 cm. longis breviter tomentosis, cincinnis subsessilibus sub anthesi plerumque unifloris, bracteis lanceolatis circiter 1 mm. longis dorso breviter hispidis, pedicellis gracilibus glabris sub anthesi circiter 1.5 mm. longis; sepalis 4 membranaceis late rotundatis, 1–1.3 mm. longis, interioribus circiter 2 mm. longis, exterioribus minoribus, margine obscure ciliolato excepto glabris; petalis 4 membranaceis obovatis, 1–1.2 mm. longis et latis, infra medium gradatim angustatis, undulato-marginatis et apice leviter emarginatis, supra unguem margine incurvatis et pilis circiter 0.3 mm. longis conspicue hirsutis; disci glandulis subcarnosis semiorbicularibus circiter 0.4 mm. diametro parce pilosis; staminibus 8, filamentis filiformibus circiter 1.5 mm. longis villosis, antheris subgloboso-oblongis circiter 0.4 mm. longis; pistilli rudimento villoso.

VITI LEVU: Tholo North: Nandarivatu, alt. 1000 m., *Gillespie 4160* (A—TYPE, Bish), Dec. 3, 1927 (small tree, in dark woods on stream above swimming pool; native name: *si ta*).

Allophylus umbrinus is very closely allied to *A. sublaxus* Gillespie, its flowers differing only in the villose rather than glabrous filaments. However, the new species is readily distinguished by the conspicuous soft pubescence of its branchlets, petioles, leaflet-blades, and inflorescence branches. In *A. sublaxus* these parts are glabrous, or at least subglabrate and never more than inconspicuously puberulent.

ALLOPHYLUS TIMORENSIS (DC.) Bl. Rumphia **3**: 130. 1847; Radlk. in Pflanzenr. 98b (IV. **165**): 587. 1932.

KAMBARA: Limestone formation, alt. 0–100 m. *Smith 1287* (Bish, GH) (slender shrub 2 m. high, in thickets; fruit red; native name: *sendamu*). FULANGA: Limestone formation, alt. 0–80 m., *Smith 1111* (Bish, GH) (tree 8 m. high, in forest; petals and stamens white), *1161* (Bish, GH) (shrub 2 m. high, in thickets; stamens white).

Although this widespread and common species has been extensively reported from the adjacent groups, such as the New Hebrides and Samoa, it has apparently escaped previous notice in Fiji.

RHAMNACEAE

RHAMNELLA Miq. Ann. Mus. Bot. Lugd.-Bat. **3**: 30. 1867.

Dallachya F. v. Muell. Fragm. Phyt. Austral. **9**: 140. 1875; syn. nov.

Because the genus *Rhamnella* has not previously been reported east of continental Asia, Japan, and Hainan, the reduction of *Dallachya* to its synonymy is proposed only after careful consideration of generic lines in the Tribe Zizypheae. *Dallachya*, a montoypic genus based on *Rhamnus vitiensis* Benth., was originally placed in the vicinity of *Ventilago* Gaertn. and *Smythea* Seem., but the fruit immediately excludes it from the Tribe Ventilagineae. Weberbauer (in E. & P. Nat. Pfl. **3**(5): 407. 1895) mentions *Dallachya* as a genus of uncertain position, probably belonging in the Tribe Zizypheae. In the characters of its flowers and fruits, *Dallachya vitiensis* seems to be practically indistinguishable, even in the smallest details, from several species of *Rhamnella* as interpreted by C. Schneider (in Sargent, Pl. Wils. **2**: 222–226. 1914).

The Australian-Pacific species is apparently closest to *R. rubrinervis* (Lévl.) Rehder [*R. hainanensis* Merr.], from which it differs in its glabrous habit, details of its leaf-margin and venation, and its strictly fasciculate flowers and fruits.

Rhamnella vitiensis (Benth.) A. C. Sm., comb. nov. *Colubrina vitiensis* Seem. Mission to Viti 434, nomen. 1862. *Rhamnus vitiensis* Benth. Fl. Austral. **1**: 413. 1863; Seem. Fl. Vit. 42. 1865; Warb. in Bot. Jahrb. **13**: 368. 1891; Burkill in Jour. Linn. Soc. Bot. **35**: 32. 1901. *Berchemia Fournieri* Panch. & Seb. in Seb. Not. Bois Nouv. Cal. 236. 1874; Guillaumin in Ann. Mus. Col. Marseille II. **9**: 120. 1911; Schinz & Guillaumin in Sarasin & Roux, Nova Cal. Bot. **1**: 174. 1920; Guillaumin in Jour. Arnold Arb. **12**: 238. 1931; Daniker in Vierteljahres. Nat. Ges. Zurich **78**: Beibl. 19: 251. 1933. *Dallachya vitiensis* F. v. Muell. Fragm. Phyt. Austral. **9**: 140. 1875; Weberb. in E. & P. Nat. Pfl. **3**(5): 407. 1895; Lauterb. & K. Schum. Fl. Deutsch. Schutzgeb. Südsee 426. 1901; Lauterb. in Bot. Jahrb. **57**: 330. 1922. *Berchemia crenulata* Panch. ex Guillaumin in Ann. Mus. Col. Marseille II. **9**: 120, nomen. 1911.

From the specific epithet, one would naturally expect this species to be typified by a Fijian collection, but this is not the case. Seemann's mention of *Colubrina vitiensis* refers to his no. *85*, but there is no description and therefore the name has no standing. The same collection had already been mentioned by Gray (in Proc. Am. Acad. **5**: 316. 1862, in Bonplandia **10**: 35. 1862) as a probably new species of Rhamnaceae, but without definite mention of a genus. Therefore Bentham's description in 1863 must be taken as the basis of the binomial. This description appears to have been based entirely on a MacGillivray collection from Cape York, Queensland. Bentham cites *Colubrina vitiensis* Seem. as a synonym and remarks: "Apparently the same species was gathered in the Fiji Islands by Seemann, and his specimens have young fruits, of an obovoid-oblong shape, which, as far as they go, agree with those of *Rhamnus*."

Fortunately Bentham appears to have been correct in his belief that the Australian and Fijian plants are conspecific; at least, on the basis of the collections now available, I cannot distinguish the Pacific from the Australian material. The species has been reported from Queensland, New Guinea, New Caledonia, the Loyalty Islands, the New Hebrides, Fiji, and Tonga. I have seen the following Fijian specimens:

VITI LEVU: Lautoka: North of Lomolomo, alt. 90 m., *Degener & Ordonez 13713* (A) (tree 3 m. high, in dry forest). KANDAVU: Hills above Namalata and Ngaloa Bays, alt. 200–400 m., *Smith 123* (Bish, GH) (scandent shrub, in forest; anthers yellowish). FULANGA: Limestone formation, alt. 0–80 m., *Smith 1113* (Bish, GH) (gnarled tree 3 m. high, on cliffs; flowers pale yellow; native name: *taka*). WITHOUT DEFINITE LOCALITY: *Seemann 85* (source of the name *Colubrina vitiensis* Seem., GH). Mr. William Greenwood informs me that he has collected this species at Lautoka and also at Lambasa, Mathuata, Vanua Levu.

My conclusions as to the specific identity of plants from various Pacific and Australian regions are based upon examination of the following collections:

QUEENSLAND: Rockingham Bay, *Dallachy* (GH); Palm Island, *Bancroft* (A); Daintree River, alt. 10 m., *Kajewski 1401* (A), *1464* (A) (common vines on rain-forest trees; fruit black when ripe, up to 9 by 7 mm.). NEW CALEDONIA: *Balansa 959* (A); *Le Rat 66* (A). NEW HEBRIDES: Aneityum: Anelgauhat Bay, alt. 30 m., *Kajewski 738* (A).

COLUBRINA PAPUANA Merr. & Perry in Jour. Arnold Arb. **22**: 264. 1941.

VITI LEVU: Tholo North: Nandarivatu, alt. about 900 m., *Greenwood 856* (A) (tree about 13 m. high; trunk 45 cm. diam.; young fruits yellow); Tholo East: Taulevu-Vunindawa track, alt. about 150 m., *B. E. Parham 741* (A) (shrub 3 m. high, in grassland); Naitasiri: Nasinu, 9 miles from Suva, alt. 150 m., *Gillespie 3599.9* (Bish), *3661* (A, Bish) (tree 10 m. high, copiously branching; trunk 12 cm. diam.; fruit dull russet-green, the seeds orange-red). WITHOUT DEFINITE LOCALITY. *Horne 1116* (Bish).

The cited specimens, all of which are in fruit, appear to me quite identical with the three New Guinean specimens cited in connection with the original description. There seems no doubt as to the place of the plant in *Colubrina;* the fruit-shape and the method of dehiscence suggest the common *C. asiatica* (L.) Brongn., from which *C. papuana* is at once distinguished by its different foliage and larger fruits with thicker valves and larger seeds. The occurrence of this New Guinean species in Fiji is surprising, but possibly future collections in the Solomons and the New Hebrides will solidify the range. It is possible, of course, that discovery of flowering material in Fiji will make specific recognition of our plant advisable, but in view of the remarkable similarity of our material to that of New Guinea, in foliage and fruit, I doubt if such separation will prove feasible.

FLACOURTIACEAE

Xylosma Bryanii A. C. Sm., sp. nov.

Frutex inermis parvus ad 1 m altus, ramulis gracilibus subteretibus obscure lenticellatis et petiolis juventute obscure puberulis demum glabrescentibus; petiolis gracilibus leviter canaliculatis 3–5 mm. longis; laminis chartaceis glabris in sicco fuscis obovatis vel elliptico-obovatis, (1.5–) 2–3 cm. longis, 1–2.2 cm. latis, basi acutis vel obtusis et in petiolum inconspicue decurrentibus, apice rotundatis, margine integris et conspicue sed anguste revolutis, subtus dense et minute glanduloso-ceriferis, costa supra prominula subtus elevata, nervis secundariis utrinsecus 2 vel 3 adscendentibus anastomosantibus utrinque prominulis, rete venularum utrinque obscure prominulo; inflorescentiis ♀ solis visis axillaribus breviter racemosis 2–4-floris, rhachi

2–3 mm. longa puberula, bracteis ovato-deltoideis subacutis puberulis circiter 1 mm. longis et 0.7 mm. latis, pedicellis gracilibus 5–6 mm. longis obscure puberulis; sepalis 4 submembranaceis ovatis vel ellipticis, sub anthesi circiter 2 mm. longis et latis sub fructu paullo majoribus et persistentibus, apice rotundatis vel obtusis (interioribus interdum 2- vel 3-lobatis), extus glabris vel obscure et minute puberulis, intus dense pallido-sericeo-puberulis; disco parvo obscure crenulato; ovario glabro ovoideo sub anthesi circiter 1.5 mm. longo, stylo brevi crasso, placentis 2 inconspicuis, ovulis circiter 4 per placentam, stigmate obscure lobato; fructibus ovoideis vel ellipsoideis, maturitate 8–9 mm. longis et 5–7 mm. latis, stylo circiter 1 mm. longo coronatis, pericarpio crasso-carnoso, placentis oppositis, seminibus circiter 5 castaneis ovoideis, circiter 3.5 ab 2.5 mm., basi obtusis, apice rotundatis.

ONGEA: Rocky islet off shore of Ongea ndriti, alt. 10–20 m., *Bryan 392* (A—fragm., Bish—TYPE), July 26, 1924 (small shrub, 0.5–1 m. high; flowers green and white; fruit green to purple).

Xylosma Bryanii is very distinct among Pacific species, being distinguished by its diminutive habit, small revolute-margined leaf-blades, compact inflorescences, and ovaries with two placentas. In Sleumer's treatment (in Notizbl. Bot. Gart. Berlin **14**: 288–297. 1938) it may be placed near *X. ovatum* Benth. of Australia, a species with slightly larger leaves, more numerous flowers, shorter pedicels, smaller sepals, more prominent placentas, and fewer ovules.

It is a pleasure to name the new species for the collector, Dr. E. H. Bryan, Jr., Curator of the Bernice P. Bishop Museum.

XYLOSMA ARCHBOLDIANUM A. C. Sm. in Sargentia **1**: 61. 1942.

VITI LEVU: Rewa: Korombamba Mt., alt. about 420 m., *B. E. Parham 1269* (A) (shrub, in forest).

The second collection of this recently described species, collected near the southeastern rather than the northeastern coast of Viti Levu, bears mature staminate flowers and is slightly more robust than the type, with which it is identical in all essential characters. The following amplification of the original description is now possible:

Frutex, petiolis ad 12 mm. longis, laminis ad 8 cm. longis et 5 cm. latis; inflorescentiis ♂ maturis axillaribus solitariis racemosis 7- vel 8-floris, rhachi gracili circiter 7 mm. longa, bracteis ovato-deltoideis subacutis 0.5–0.7 mm. longis et latis; pedicellis gracilibus sub anthesi 3–5 mm. longis, supra basim 1–2.5 mm. articulatis; sepalis 4–6 (1 vel 2 exterioribus oblongis minoribus saepe deficientibus) intus pallide pilosis, late ovatis, 0.7–1.3 mm. longis, 1.4–1.6 mm. latis, apice rotundatis vel mucronulatis; toro complanato disco incluso 1.5–2 mm. diametro; staminibus circiter 40, filamentis gracilibus glabris 1.5–2 mm. longis, antheris oblongis circiter 0.5 mm. longis et latis.

BARRINGTONIACEAE

BARRINGTONIA PETIOLATA A. C. Sm. in Bishop Mus. Bull. **141**: 102. *f. 54.* 1936; Knuth in Pflanzenr. 105 (IV. **219**): 36. 1939.

VITI LEVU: Tholo West: Mbuyombuyo, near Namboutini, *Tabualewa 15612* (A) (tree 13 m. high, in forest); Naitasiri: Mt. Kombalevu, alt. 350 m., *Parks 20309* (Bish) (tree 15 m. high, in thick bush); vicinity of Nasinu, 9 miles from Suva, alt. 150 m., *Gillespie 3584* (A, Bish) (in woods; flowers pink).

This species has previously been recorded only from the three specimens from Vanua Levu originally mentioned.

MYRSINACEAE

Discocalyx sylvestris A. C. Sm., sp. nov.

Arbor ad 10 m. alta ubique praeter inflorescentiae ramulos et calyces obscure furfuraceos glabra, ramulis gracilibus cinereis teretibus rugulosis; petiolis 6–10 mm. longis superne anguste alatis; laminis chartaceis siccitate fusco-olivaceis subtus pallidioribus, obovatis, 4.5–7 cm. longis, 2.5–4 cm. latis, basi attenuatis et in petiolum decurrentibus, apice rotundatis, margine integris et minute recurvatis, costa supra subplana subtus elevata, nervis lateralibus utrinsecus 5–8 patentibus immersis interdum subtus leviter prominulis, venulis obscuris immersis; inflorescentiis axillaribus compacte paniculatis ad 3 cm. longis, ramulis gracilibus minute furfuraceis, bracteis oblongis 1.5–2 mm. longis caducis, pedicellis gracilibus sub anthesi 2–3 mm. longis parce furfuraceis; floribus ut videtur hermaphroditis; calyce rotato circiter 2 mm. diametro profunde 5-lobato utrinque glabro vel extra obscure furfuraceo, lobis deltoideo-oblongis parce glanduloso-punctatis, 0.5–0.8 mm. longis et latis, apice obtusis vel rotundatis, margine copiose et breviter brunneo-ciliolatis; corolla rotata 4–4.5 mm. diametro fere ad basim 5-lobata, lobis oblongis circiter 1.5 mm. longis et latis apice rotundatis nigro-glanduloso-punctatis; staminibus quam pistillo brevioribus, antheris sessilibus oblongo-ovoideis circiter 0.7 mm. longis obscure glandulosis apice obtusis; pistillo sub anthesi circiter 1.3 mm. longo glabro, ovario graciliter ovoideo in stylum crassum circiter 0.5 mm. longum attenuato, stigmate subpentagono, ovulis plerumque 3; fructu subgloboso 4–5 mm diametro obscure glanduloso-lineolato, stylo persistente coronato.

VITI LEVU: Rewa or Naitasiri: Central Road, near Suva, alt. 250 m., *MacDaniels 1131* (A—TYPE, Bish), Apr. 13, 1927 (tree 10 m. high, the trunk 15 cm diam.; in rain-forest).

Discocalyx sylvestris appears to be closely related only to *D. multiflora* Gillespie, from which it differs in its shorter and proportionately broader leaf-blades with fewer and more obscure secondaries, its much more compact inflorescences, larger bracts, smaller and more deeply lobed corolla, and smaller anthers. Possibly the new species is also represented by *MacDaniels 1070* (Bish), from the coast 4 miles west of Suva, Rewa, Viti Levu, a sterile specimen with thinner punctate leaf-blades and more obvious venation.

Rapanea crassiramea A. C. Sm., sp. nov.

Arbor paullo post anthesin ubique glabra, ramulis subrectis crassissimis apicem versus 5–10 mm. diametro subteretibus fusco-cinereis copiose lenticellatis, cicatricibus foliorum delapsorum numerosis; petiolis crassis supra paullo complanatis 12–22 mm. longis; laminis coriaceis siccitate fuscis anguste obovatis, 11–15 cm. longis, 4.5–7 cm. latis, basim versus gradatim angustatis et basi ipso obtusis, apice late obtusis et saepe leviter emarginatis, margine saepe anguste recurvatis, costa supra paullo subtus valde prominente, nervis secundariis utrinsecus 12–15 cum aliis debilioribus interspersis erecto-patentibus anastomosantibus utrinque valde prominulis, rete venularum subimmerso vel subprominulo; inflorescentiis secus ramulos in axillis foliorum delapsorum copiose dispositis, e ramulis crassis verruciformibus ad

7 mm. longis et 4 mm. latis formatis plerumque 2–4-floris; pedicellis crassis circiter 1 mm. diametro 4–6 mm. longis; calyce cupuliformi tenuiter carnoso fere ad basim 5–7 (plerumque 6)-lobato, lobis deltoideis circiter 1.5 mm. longis et latis, apice subacutis vel obtusis, margine copiose sed minute glanduloso-ciliolatis; corolla staminibusque non visis; ovario post anthesin depresso-subgloboso 1.5–2 mm. diametro, stigmate ut videtur punctiformi, placenta depresso-globosa, ovulis circiter 5.

VITI LEVU: Tholo North: Nandarivatu, on wooded slopes at 900 m. alt., *Gillespie 4374* (A—fragm., Bish—TYPE), Dec. 16, 1927.

Rapanea crassiramea is a species without close allies in Fiji or the adjacent groups, characterized by its stout branchlets, large coriaceous obviously nerved leaf-blades, numerous coarse inflorescence-stalks, long pedicels, and apparently predominantly 6-merous flowers. Its foliage suggests that of some of the Polynesian species described by Mez under his numbers 61–67 (in Pflanzenr. 9 [IV. **236**]: 372, 373. 1902), but those usually have 4-merous flowers and more highly connate sepals.

OLEACEAE

Linociera Gillespiei A. C. Sm., sp. nov.

Arbor sub fructu ubique glabra, ramis ramulisque pallide cinereis gracilibus subteretibus sparse lenticellatis nodis leviter incrassatis; foliis oppositis apicem ramulorum versus 0.5–3.5 cm. distantibus, petiolis rugulosis leviter canaliculatis 10–15 mm. longis gracilibus (circiter 1.5 mm. diametro), laminis coriaceis in sicco olivaceis vel supra pallidioribus lanceolato-ellipticis, 10–14.5 cm. longis, 2.7–4 cm. latis, basi gradatim acutis et in petiolum decurrentibus, apice caudato-acuminatis (acumine 7–15 mm. longo obtuso), margine leviter recurvatis, subtus siccitate inconspicue rugulosis, costa supra subplana subtus prominente, nervis lateralibus utrinsecus 5–8 arcuato-adscendentibus marginem versus anastomosantibus supra planis vel leviter insculptis subtus valde elevatis, rete venularum obscuro vel subtus paullo prominulo; infructescentiis axillaribus (?) ut videtur racemosis circiter 2 cm. longis, rhachi rugosa circiter 3 mm. diametro, pedicellis non visis; fructu siccitate coriaceo ellipsoideo obtuse circumcarinato, basi et apice rotundato, circiter 33 ab 20 ab 16 mm., pericarpio valde ruguloso, vivo forsan crasse carnoso.

VITI LEVU: Tholo North: Vicinity of Nandarivatu, near summit of Loma Langa Mt., alt. 1150 m., *Gillespie 4289* (A—fragm., Bish—TYPE), Dec. 13, 1927.

The only species of *Linociera* which has been reported from Fiji or adjacent groups to the east is *L. pauciflora* C. B. Clarke, mentioned by Burkill (in Jour. Linn. Soc. Bot. **35**: 45. 1901) as occurring in Fiji and Tonga. However, neither of the species here described as new is closely related to *L. pauciflora*, which is based on a specimen from Penang and which doubtfully extends into the Pacific. The only species thus far reported from the New Hebrides is *L. ramiflora* Wall., not a close relative of either of the new species. *Linociera sessiliflora* Hemsl., from Papuasia and Micronesia, has leaves resembling those of *L. Gillespiei* in shape and texture, but with much shorter petioles. The inflorescence of *L. sessiliflora* is fasciculate and compact, whereas both *L. Gillespiei* and *L. vitiensis* (below described), as far

as can be ascertained from fruiting specimens, have racemose inflorescences and thus might be better placed in Lingelsheim's *Racemosae* (in Bot. Jahrb. **61**: 6, 7. 1927). The actual relationships of the two new Fijian species cannot yet be definitely established, but they are well characterized by their short and presumably racemose inflorescences and large fruits.

Linociera vitiensis A. C. Sm., sp. nov.

Arbor 5 m. alta sub fructu ubique glabra, ramulis cinereis vel distaliter pallide fuscis conspicue lenticellatis subteretibus, apicem et nodos incrassatos versus complanatis; foliis oppositis 2–3 cm. distantibus, petiolis castaneis rugulosis canaliculatis 12–16 mm. longis 1–1.5 mm. diametro, laminis coriaceis olivaceis concoloribus late ellipticis, 7–10 cm. longis, 4.5–5.5 cm. latis, basi in petiolum abrupte attenuatis, apice obtuso-cuspidatis vel subito in acumine obtuso ad 9 mm. longo acuminatis, margine paullo recurvatis, costa supra subplana subtus prominente, nervis lateralibus utrinsecus plerumque 5 erecto-patentibus intra marginem anastomosantibus supra leviter insculptis subtus elevatis, venulis immersis vel subtus inconspicue prominulis; infructescentiis axillaribus vel e ramulis infra folia orientibus racemosis circiter 2 cm. longis, rhachi circiter 2 mm. diametro, pedicellis paucis valde rugosis incrassatis 3–4 mm. longis; fructu siccitate coriaceo (vivo carnoso luteo) ellipsoideo obtuse circumcarinato, basi et apice rotundato, circiter 30 ab 17 ab 14 mm., pericarpio valde ruguloso, vivo levi.

TAVEUNI: Borders of lake east of Somosomo, alt. 700–900 m., *Smith 861* (Bish, GH—TYPE), Dec. 29, 1933 (tree 5 m. high, in dense forest on island in swamp; fruit yellow; native name: *lolovata*).

Linociera vitiensis is doubtless a close relative of the preceding new species, *L. Gillespiei*, the two being readily distinguished by obvious foliage characters.

APOCYNACEAE

Bleekeria vitiensis (Markgraf) A. C. Sm., comb. nov. *Excavatia vitiensis* Markgraf in Bishop Mus. Bull. **141**: 127. *f. 66, b, c.* 1936.

Merrill and Perry (in Jour. Arnold Arb. 24: 213. 1943), in a recent discussion of *Bleekeria* Hasskarl, point out that *Excavatia* Markgraf (in Bot. Jahrb. **61**: 195. 1927) represents the same concept. Many of the necessary transfers from the inclusive genus *Ochrosia* Juss. to *Bleekeria* were made by Koidzumi in Bot. Mag. Tokyo **37**: 52. 1923. Among these combinations, which are not in general herbarium use, is *Bleekeria elliptica* (Labill.) Koidz. for the well-known *Ochrosia elliptica* Labill., which occurs in Fiji. This species was inconspicuously transferred to *Excavatia* by Markgraf as *Excavatia elliptica* (Labill.) Markgraf, in Bishop Mus. Bull. **141**: 128. 1936.

ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)
(See also under General Botany. **Standley & Steyermark**)

Allard, H. A. The eastern false mistletoe (*Phoradendron flavescens*); when does it flower? Castanea **8:** 72–78. Ap 1943.

Ames, O. & Correll, D. S. A new *Epidendrum* from Guatemala. Am. Orchid Soc. Bull. **12:** 60. *pl. 2.* 6 Jl 1943.

Ames, O. & Correll, D. S. Studies in *Habenaria* and *Dichaea.* Bot. Mus. Leafl. **11:** 57–80. *pl. 4, 5.* 27 My 1943.

Anderson, L. E. The distribution of *Tortula pagorum* (Milde) de Not. in North America. Bryologist **46:** 47–66. Je 1943.

Anderson, W. A. Notes on Iowa flora. Proc. Iowa Acad. **49:** 205. 1942. [My 1943].

Babel, W. K. The variations of *Brachyelytrum erectum.* Rhodora **45:** 260–262. 29 My 1943.

Ball, C. R. Illustrating plant organs for taxonomic purposes. Castanea **8:** 67–71. Ap 1943.

Barkley, F. A. Anacardiaceae Lindl. *In:* Flora of Texas **3:** 89–108. Southern Methodist University [Jl] 1943.

Bomhard, M. L. Distribution and character of *Sabal louisiana.* Jour. Wash. Acad. **33:** 170–182. *pl. 1–2, f. 1.* 15 Je 1943.

Britton, M. E. Notes on the distribution of some rarely reported species of *Oedogonium.* Trans. Ill. Acad. **35:** 58, 59. D 1942.

Clausen, R. T. *Scabiosa Columbaria* in central New York. Rhodora **45:** 220, 221. 29 My 1943.

Clausen, R. T. Two *Botrychium* records. Am. Fern Jour. **33:** 70. Ap–Je 1943.

Conard, H. S. The liverworts of Iowa. Proc. Iowa Acad. **49:** 191–195. 1942. [My 1943].

Cory, V. L. A new *Streptanthus* from the Big Bend of Texas. Rhodora **45:** 258–260. 29 My 1943.

Croizat, L. *Navajoa,* a new genus in Cactaceae. Cact. & Succ. Jour. **15:** 88, 89. *f. 42.* Je 1943.

Croker, D. M. A key to the Illinois species of *Solidago.* Trans. Ill. Acad. **35:** 62, 63. D 1942.

Cronquist, A. The identity of *Aster salsuginosus* Richardson. Rhodora **45:** 262–264. 29 My 1943.

Cuatrecasas, J. Estudios sobre plantas andinas—IV. Caldasia **6:** 5–9. *f. 1.* 15 Mr 1943.

Daily, W. A. First reports for the algae *Borzia*, *Aulosira* and *Asterocytis* in Indiana. Butler Univ. Bot. Stud. **6:** 84–86. My [Je] 1943.

Demaree, D. Arkansas fern notes. Am. Fern Jour. **33:** 75. Ap–Je 1943.

Drexler, R. V. A preliminary list of bryophytes of Linn County, Iowa. Proc. Iowa Acad. **49:** 197–204. 1942 [My 1943].

Dugand, A. Notas sobre el genero de palmas *Cuatrecasea*. Caldasia **6:** 69–73. 15 Mr 1943.

Dugand, A. Nuevas especies de *Ficus* de Colombia y del Ecuador. Caldasia **6:** 77–80. 15 Mr 1943.

Dugand, A. Revalidacion de *Bombax ceiba* L. como especie tipica del genero *Bombax* L. y descripcion de *Pseudobombax* gen. nov. Caldasia **6:** 47–68. 15 Mr 1943.

Dugand, A. Una palma nueva del genero *Desmoncus*. Caldasia **6:** 75, 76. 15 Mr 1943.

Egler, F. E. The ferns and flowering plants of the Clark Reservation, Onondaga County, New York. N. Y. Coll. Forestry Tech. Publ. 61: 1–64. *f. 1–3.* My 1943.

Feldman, A. W. Trees and shrubs of Champaign County, Illinois. Trans. Ill. Acad. **35:** 60, 61. D 1942.

Fernald, M. L. Contributions from the Gray Herbarium of Harvard University—No. CXLVIII. I. Five common rhizomatous species of *Muhlenbergia*. Rhodora **45:** 231–239. *pl. 749–757.* 29 My 1943. II. Notes on *Danthonia*. 239–246. III. *Erianthus brevibarbis* and other species. 246–255. *pl. 758–761.* IV. Why not *Andropogon Gerardi?* 255–258.

Fernald, M. L. Contributions from the Gray Herbarium of Harvard University—No. CXLVIII. V. Studies in North American species of *Scirpus*. Rhodora **45:** 279–296. *pl. 762–767.* Jl 1943. VI. The identity of *Scleria setacea* of Poiret. 296, 297. VII. What is *Angelica triquinata?* 298–303. *pl. 768, 769.*

Fernald, M. L. Our varieties of *Barbarea vulgaris*. Rhodora **45:** 304. Jl 1943.

Fosberg, F. R. Notes on North American plants. IV. Am. Midl. Nat. **29:** 785, 786. My [Je] 1943.

Friesner, R. C. Two *Solidago* hybrids worthy of names. Butler Univ. Bot. Stud. **6:** 81–83. My [Je] 1943.

Gilly, C. L. Studies in the Sapotaceae, III. A new species of *Manilkara* from Cuba. Trop. Woods **94:** 15–17. 1 Je 1943.

Glassman, S. A taxonomic study of the Illinois species of *Rumex*. Trans. Ill. Acad. **35:** 63–65. D 1942.

Goodman, G. J. Notes on Iowa plants. Proc. Iowa Acad. **49:** 207–209. 1942. [My 1943].

Goodman, G. J. & Leyendecker, P. J. The genus *Lysimachia* in Iowa. Proc. Iowa Acad. **49:** 211, 212. 1942 [My 1943].

Gorham, R. P. The distribution of *Prunus nigra* Ait. in New Brunswick. Acadian Naturalist **1:** 43–46. My 1943.

Gorham, R. P. A new location for *Shepherdia canadensis*. Acadian Naturalist **1:** 48, 49. My 1943.

Harris, S. K. Plants of the Presidential Range, IV. Primrose, Mint, Figwort, Madder, Honeysuckle, and Bluebell families. Appalachia NS **9:** 360–367. *illust.* Je 1943.

Hopkins, M. Notes from the Bebb Herbarium of the University of Oklahoma —II. Rhodora **45:** 265–277. Jl 1943.

Jones, G. N. A checklist of the vascular plants of the University of Illinois woodlands. Trans. Ill. Acad. **35:** 71, 72. D 1942.

Kelso, L. Plants of Dewer and vicinity. Biological Leaflet **19:** 1–15. 31 My 1943.

Legg, W. C. *Lygodium palmatum* in West Virginia. Am. Fern Jour. **33:** 70. Ap–Je 1943.

[Lundell, C. L.] Aquifoliaceae DC. *In:* Flora of Texas **3:** 112–122. Southern Methodist University [Jl] 1943.

[Lundell, C. L.] Cyrillaceae Lindl. *In:* Flora of Texas **3:** 109–111. Southern Methodist University [Jl] 1943.

McInteer, B. B. Algae of Kentucky: Additions to check list, II. Castanea **8:** 65, 66. Ap [Je] 1943.

McVaugh, R. Edward Palmer's collections in Arizona in 1869, 1876 and 1877. Part 1. General discussion: itinerary and sources. Am. Midl. Nat. **29:** 768–775. My [Je] 1943.

McVaugh, R. & Kearney, T. H. Edward Palmer's collections in Arizona in 1869, 1876 and 1877. Part 2. A consideration of some Palmer collections cited in the "Flowering Plants and Ferns of Arizona." Am. Midl. Nat. **29:** 775–778. My [Je] 1943.

Merrill, E. D. New names for ferns and fern allies proposed by C. S. Rafinesque 1806–1838. Am. Fern Jour. **33:** 41–56. Ap–Je 1943.

Moran, R. A revision of *Dudleya*, subgenus *Stylophyllum*—V. Desert **15:** 56–60. *f. 11–13.* Ap 1943.

Palmer, E. J. *Quercus Prinus* Linnaeus. Am. Midl. Nat. **29:** 783, 784. My [Je] 1943.

Proctor, G. R. *Pellaea glabella* in Adams County, Ohio. Am. Fern Jour. **33:** 71. Ap–Je 1943.

Record, S. J. Keys to American woods. Trop. Woods **74:** 17–43. 1 Je 1943.

Rice, M. A. Bryophytes in the vicinity of Wheaton College, Norton, Massachusetts. Bryologist **46:** 66–71. Je 1943.

St. John, E. P. More about the distribution of ferns in Florida. Am. Fern Jour. **33:** 59–67. Ap–Je 1943.

Schultes, R. E. Plantae Austro-Americanae—I. Caldasia **6:** 11–26. *f. 1–4.* 15 Mr 1943.

Schultes, R. E. Plantae Colombianae—III. Caldasia **6:** 27–45. *f. 1–7.* 15 Mr 1943.

Schweinfurth, C. A *Catasetum* new to Peru. Am. Orchid Soc. Bull. **12:** 18–20. *pl. 1.* 1 Je 1943.

Senn, H. A. The relation of anatomy and cytology to the classification of the Leguminosae. Chron. Bot. **7:** 306–308. Je 1943.

Setchell, W. A. *Mastophora* and the Mastophoreae: genus and sub-family. Proc. Nat. Acad. **29:** 127–135. 15 My 1943.

Shinners, L. H. Notes on Wisconsin grasses—III. *Agrostis, Calamagrostis, Calamovilfa.* Am. Midl. Nat. **29:** 779–782. My [Je] 1943.

Stiles, N. L. & Bakke, A. L. The cut-leaved nightshade (*Solanum triflorum* Nutt.). Proc. Iowa Acad. **49:** 213, 214. 1942 [My 1943].

Tehon, L. R. The white-bracted *Hymenopappus* still grows in Illinois. Trans. Ill. Acad. **35:** 78. D 1942.

Thomson, J. W. *Parmelia stygia* (L.) Ach. in New Jersey. Bryologist **46:** 46. Je 1943.

Waters, C. E. *Equisetum praealtum* in dry soil. Am. Fern Jour. **33:** 73–75. Ap–Je 1943.

Weatherby, C. A. The type species of *Cheilanthes*. Am. Fern Jour. **33:** 67–69. Ap–Je 1943.

Welch, W. H. The systematic position of the genera *Wardia, Hydropogon*, and *Hydropogonella*. Bryologist **46:** 25–46. *f. 1–39*. Je 1943.

Wheeler, L. C. History and orthography of the celastraceous genus "*Pachystima*" Rafinesque. Am. Midl. Nat. **29:** 792–795. My [Je] 1943.

Woodson, R. E. & Schery, R. W. *et al.* Flora of Panama. Part II Fascicle I (Cycadaceae-Gramineae). Ann. Mo. Bot. Gard. **30:** 97–280. *f. 1–31*. Ap [Je] 1943.

Yuncker, T. G. Convolvulaceae Lindl. 1. *Cuscuta* [Tourn.] L. *In:* Flora of Texas **3:** 123–150. *f. 1–20*. Southern Methodist University. [Jl] 1943.

MORPHOLOGY

(including anatomy, and cytology in part)

Anderson, E. & Hubricht, L. The histological basis of a specific difference in leaf texture. Am. Nat. **77:** 285–287. My–Je 1943.

Beal, J. M. & Ownbey, M. Cytological studies in relation to the classification of the genus *Calochortus*. III. Bot. Gaz. **104:** 553–562. *f. 1–11*. 30 Je 1943.

Bloch, R. The problem of polarity in plant morphogenesis. Chron. Bot. **7:** 297–299. Je 1943.

Bose, S. R. Role of pyrenoids in algae and of vacuoles in plastids of higher plants and in fungi. Bot. Gaz. **104:** 633–638. *f. 1–4*. 30 Je 1943.

Chin, T. C. Cytology of the autotetraploid rye. Bot. Gaz. **104:** 627–632. *f. 1–13*. 30 Je 1943.

Craft, J. H. Extra floral nectaries in *Bryophyllum calycinum*. Proc. Iowa Acad. **49:** 113–115. *f. 1–4*. 1942 [My 1943].

Dean, H. L. Total length of stem developed from a single seedling of *Cuscuta*. Proc. Iowa Acad. **49:** 127, 128. 1942 [My 1943].

Finkelstein, M. A study of the vascular pathways of the rhizome and base of stipe of *Dryopteris marginalis* (Linné) Asa Gray. Am. Jour. Pharm. **115:** 126–136. *f. 1–66*. Ap 1943.

Friesner, R. C. Correlation of elongation in primary, secondary and tertiary axes of *Pinus strobus* and *P. resinosa*. Butler Univ. Bot. Stud. **6:** 1–9. My [Je] 1943.

Havis, A. L. A developmental analysis of the strawberry fruit. Am. Jour. Bot. **30:** 311–314. *f. 1–4*. 25 My 1943.

Katz, E. J. Pollen-tube development in *Taraxacum officinale*. Bot. Gaz. **104:** 650, *f. 1, 2*. 30 Je 1943.

McMenamin, J. P. A microanalysis of the epidermal cell walls beneath the midrib of the holly leaf. Trans. Ill. Acad. **35:** 69, 70. D 1942.

O'Mara, J. G. Meiosis in autotetraploid *Secale cereale*. Bot. Gaz. **104:** 563–575. *f. 1–9*. 30 Je 1943.

Wylie, R. B. The dwarf leaf of *Cercis canadensis*. Proc. Iowa Acad. **49:** 117–122. 1942 [My 1943].

Wylie, R. B. A note on axis restoration in a gymnosperm tree. Proc. Iowa Acad. **49:** 123–125. *f. 1*. 1942 [My 1943].

Wylie, R. B. The role of the epidermis in foliar organization and its relations to the minor venation. Am. Jour. Bot. **30:** 273–280. *f. 1–11*. 25 My 1943.

PLANT PHYSIOLOGY

Albaum, H. G. The relationship between nitrogen transport and metabolism in the oat seedling. Am. Jour. Bot. **30:** 302–305. *f. 1–2.* 25 My 1943.

Arnon, D. I. & Hoagland, D. R. Composition of the tomato plant as influenced by nutrient supply, in relation to fruiting. Bot. Gaz. **104:** 576–590. *f. 1–7.* 30 Je 1943.

Berger, J. & Avery, G. S. Action of synthetic auxins and inhibitors on dehydrogenases of the *Avena* coleoptile. Am. Jour. Bot. **30:** 297–302. 25 My 1943.

Berger, J. & Avery, G. S. Dehydrogenases of the *Avena* coleoptile. Am. Jour. Bot. **30:** 290–297. *f. 1–7.* 25 My 1943.

Broyer, T. C. & Hoagland, D. R. Metabolic activities of roots and their bearing on the relation of upward movement of salts and water in plants. Am. Jour. Bot. **30:** 261–273. 25 My 1943.

Clark, H. E. & Kerns, K. R. Effects of growth-regulating substances on a parthenocarpic fruit. Bot. Gaz. **104:** 639–644. *f. 1, 2.* 30 Je 1943.

Flint, L. H. & Moreland, C. F. Note on photosynthetic activity in seeds of the spider lily. Am. Jour. Bot. **30:** 315–317. 25 My 1943.

Galston, A. W. The nitrogen content of oat chloroplasts. Trans. Ill. Acad. **35:** 66, 67. *f. 1.* D 1942.

Harris, D. G. & Zscheile, F. P. Effects of solvent upon absorption spectra of chlorophylls *A* and *B;* their ultraviolet absorption spectra in ether solution. Bot. Gaz. **104:** 515–527. *f. 1–4.* 30 Je 1943.

Lyon, C. B., Beeson, K. C. & Ellis, G. H. Effects of micro-nutrient deficiencies on growth and vitamin content of the tomato. Bot. Gaz. **104:** 495–514. *f. 1–3.* 30 Je 1943.

Noggle, G. R. The rate of transpiration in two oat varieties grown under varying soil moisture levels. Trans. Ill. Acad. **35:** 73, 74. *f. 1.* D 1942.

Parker, M. W. & Borthwick, H. A. Influence of temperature on photoperiodic reactions in leaf blades of Biloxi soybean. Bot. Gaz. **104:** 612–619. *f. 1.* 30 Je 1943.

Reeves, R. E. & Sisson, W. A. Chemical reactivity of cotton fiber as related to type of x-ray diffraction pattern. Contr. Boyce Thompson Inst. **13:** 11–15. *f. 1.* Ja–Mr 1943.

Reeves, R. E. Protecting cotton fiber from periodate oxidation. Contr. Boyce Thompson Inst. **13:** 1–9. *f. 1, 2.* Ja–Mr 1943.

Scofield, H. T. & Yarman, L. E. Some investigations of the water relations of lichens. Ohio Jour. Sci. **43:** 139–146. *f. 1–3.* My 1943.

Stanfield, J. F. Some growth responses of *Soja* and *Vinca* to vitamins. Trans. Ill. Acad. **35:** 75–77. *f. 1.* D 1942.

Stephenson, R. B. A preliminary investigation of the effect of naphthalene acetic acid upon the growth and composition of oats. Trans. Ill. Acad. **35:** 83, 84. *f. 1, 2.* D 1942.

Turrell, F. M. & Bauguess, L. C. Histological responses of stock (*Mathiola incana*) seedlings treated with B-indolyl acetic acid. Proc. Iowa Acad. **49:** 133–138. *f. 1–5.* 1942 [My 1943].

Turrell, F. M. & Kersten, H. A qualitative study of the effect of soft x rays on the activity of B-indolyl acetic acid as a growth substance. Proc. Iowa Acad. **49:** 139–143. *f. 1, 2.* 1942 [My 1943].

Voigt, J. W. A preliminary investigation of the effect of the descaling of winter buds on their growth in east central Illinois. Trans. Ill. Acad. **35:** 79, 80. D 1942.

Voth, P. D. Effects of nutrient-solution concentration on the growth of *Marchantia polymorpha.* Bot. Gaz. **104:** 591–601. *f. 1–3.* 30 Je 1943.

Watson, S. A. Preliminary studies on riboflavin (vitamin B_1) content of plant materials. Trans. Ill. Acad. **35:** 84, 85. D 1942.

Weiss, M. G. Inheritance and physiology of efficiency in iron utilization in soybean. Genetics **28:** 253–268. *f. 1–3.* My 1943.

GENETICS
(including cytogenetics)
(See also under Plant Physiology: Weiss)

Christensen, H. M. & Bamford, R. Haploids in twin seedlings of pepper, *Capsicum Annuum* L. Jour. Hered. **34:** 99–104. *f. 1–2.* Ap 1943.

Jodon, N. E. & Beachell, H. M. Rice dwarf mutations and their inheritance. Jour. Hered. **34:** 155–160. *f. 12–14.* My 1943.

Krug, C. A. Chromosome numbers in the subfamily Aurantioideae with special reference to the genus *Citrus.* Bot. Gaz. **104:** 602–611. *f. 1–11.* 30 Je 1943.

Myers, W. M. Analysis of variance and covariance of chromosomal association and behavior during meiosis in clones of *Dactylis glomerata.* Bot. Gaz. **104:** 541–552. 30 Je 1943.

Pope, M. N. Cleavage polyembryony in barley. Jour. Hered. **34:** 153, 154. *f. 11.* My 1943.

Rick, C. M. Cyto-genetic consequences of x-ray treatment of pollen in *Petunia.* Bot. Gaz. **104:** 528–540. *f. 1–5.* 30 Je 1943.

Rick, C. M. The x-ray induced mutation rate in pollen in relation to dosage and the nuclear cycle. Genetics **28:** 237–252. *f. 1–5.* My 1943.

Smith, H. H. Effects of genome balance, polyploidy, and single extra chromosomes on size in *Nicotiana.* Genetics **28:** 227–236. *f. 1, 2.* My 1943.

Smith, L. Relation of polyploidy to heat and x-ray effects in the cereals. Jour. Hered. **34:** 131–134. *f. 1, 2.* My 1943.

Smith, W. K. Propagation of chlorophyll deficient sweetclover hybrids as grafts. Jour. Hered. **34:** 135–140. *f. 3–5.* My 1943.

Stewart, R. N. Occurrence of aneuploids in *Lilium.* Bot. Gaz. **104:** 620–626. *f. 1–28.* 30 Je 1943.

Wagner, W. H. Hybridization by remote control. Am. Fern Jour. **33:** 71–73. Ap–Je 1943.

MYCOLOGY AND PHYTOPATHOLOGY

Bitancourt, A. A. Plant pathology in Brazil. Chron. Bot. **7:** 318–320. Je 1943.

Drechsler, C. Two new basidiomycetous fungi parasitic in nematodes. Jour. Wash. Acad. **33:** 183–189. *f. 1, 2.* 15 Je 1943.

Gilman, J. C. Illustrations of the fleshy fungi of Iowa. III. The black-spored Agarics. Proc. Iowa Acad. **49:** 153–158. *f. 1–5.* IV. Common fleshy Ascomycetes. 159–171. *f. 1–13.* 1942 [My 1943].

Gilman, R. Slime molds of Benzie County, Michigan. Proc. Iowa Acad. **49:** 189, 190. 1942 [My 1943].

Grumbein, M. L. *Typhula juncea* in Iowa. Proc. Iowa Acad. **49:** 185–187. *f. 1.* 1942 [My 1943].

Hart, H. & Allison, J. L. A browning reaction to stem rust in wheat. Phytopathology **33:** 484–496. *f. 1–5.* Je 1943.

Johann, H. *Phoma terrestris* in the roots of mature maize plants. Phytopathology **33:** 526–528. *f. 1.* Je 1943.

Johnson, H. W. & Koehler, B. Soybean diseases and their control. U.S.D.A. Farmers' Bull. 1937: 1–24. *f. 1–16.* My 1943.

Karling, J. S. The simple holocarpic biflagellate Phycomycetes. *i–x,* 1–123. *pl. 1–25. f. a–m.* New York, the author, 1942.

Keitt, G. W. & Clayton, C. N. A destructive virus disease of sour cherry. Phytopathology **33:** 449–468. *f. 1–8.* Je 1943.

Kolk, L. A. Germination of grass smuts. Am. Jour. Bot. **30:** 317–330. *pl. 1–4.* 25 My 1943.

Lentz, P. L. The genus *Thelephora* in Iowa. Proc. Iowa Acad. **49:** 175–184. *f. 1–7.* 1942 [My 1943].

Martin, G. W. Notes on Iowa fungi. IX. Proc. Iowa Acad. **49:** 145–152. 1942 [My 1943].

Smith, J. E. & Shaw, K. J. Pathogenicity studies with fusaria isolated from tobacco, sweet potato and cotton. Phytopathology **33:** 469–483. *f. 1, 2.* Je 1943.

Smith, O. F. & Allen, M. W. The bulb or stem nematode on alfalfa, sweet clover, and white clover. Phytopathology **33:** 525, 526. Je 1943.

Sparrow, F. K. Aquatic Phycomycetes exclusive of Saprolegniaceae and *Pythium. i–xix,* 1–785. *f. 1–69.* Ann Arbor, Univ. Michigan Press, 1943.

Thomas, R. C. Composition of fungus hyphae. IV: *Phytophthora.* Ohio Jour. Sci. **43:** 135–138. My 1943.

Tulk, M. Some notes on the fungi of Henry County. Proc. Iowa Acad. **49:** 173, 174. 1942 [My 1943].

PALEOBOTANY

Hansen, H. P. A pollen study of two bogs on Orcas Island, of the San Juan Islands, Washington. Bull. Torrey Club **70:** 236–243. *f. 1–2.* 1 My 1943.

Hoskins, J. H. & Cross, A. T. New interpretations of *Sphenophyllostachys* based on a petrified specimen from an Iowa coal ball. Trans. Ill. Acad. **35:** 68, 69. D 1942.

Hoskins, J. H. & Cross, A. T. Notes on a new specimen of *Lepidostrobus imbricatus* Hoskins and Cross. Am. Midl. Nat. **29:** 539–541. *f. 1–2.* Mr [Ap] 1943.

Hoskins, J. H. & Cross, A. T. *Lepidostrobus aristatus* Hoskins and Cross, a homonym. Am. Midl. Nat. **29:** 542. Mr [Ap] 1943.

Potzger, J. E. & Otto, J. H. Post-glacial forest succession in northern New Jersey as shown by pollen records from five bogs. Am. Jour. Bot. **30:** 83–87. 31 Mr 1943.

Wilson, L. R. & Cross, A. T. A study of the plant micro-fossil succession in the bottom deposits of Crystal Lake, Vilas County, Wisconsin, and the peat of an adjacent bog. Am. Jour. Sci. **241:** 307–315. *f. 1, 2.* My 1943.

ECOLOGY AND PLANT GEOGRAPHY

(See also under General Botany: **Ochoterena**)

Acosta Solis, M. Anotaciones sobre la vegetació del Norte de Quito: Desde cotocollao y San Antonio Hasta el Rio Guayllabamba. Flora **2:** 101–113. *f. 18–35.* D 1942.

Anderson, W. A. A fen in northwestern Iowa. Am. Midl. Nat. **29:** 787–791. My [Je] 1943.

Cain, S. A. Sample-plot technique applied to alpine vegetation in Wyoming. Am. Jour. Bot. **30:** 240–247. *f. 1–7.* Ap 1943.

Cook, C. W. A study of the roots of *Bromus inermis* in relation to drought resistance. Ecology **24:** 169–182. *f. 1–5.* Ap 1943.

Darlington, H. C. Vegetation and substrate of Cranberry Glades, West Virginia. Bot. Gaz. **104:** 371–393. *f. 1–17.* 31 Mr 1943.

Daubenmire, R. F. Vegetational zonation in the Rocky Mountains. Bot. Rev. **9:** 325–393. Je 1943.

Frazier, J. C. Nature and rate of development of root system of *Convolvulus arvensis.* Bot. Gaz. **104:** 417–425. *f. 1–9.* 31 Mr 1943.

Hall, T. F. & Penfound, W. T. Cypress-gum communities in the Blue Girth swamp near Selma, Alabama. Ecology **24:** 208–217. *f. 1–4.* Ap 1943.

Hansen, H. P. Paleoecology of a peat deposit in east central Washington. Northwest Sci. **17:** 35–40. My 1943.

Harris, H. L. & Drew, W. B. On the establishment and growth of certain legumes on eroded and uneroded sites. Ecology **24:** 135–148. *f. 1–8.* Ap 1943.

Hupp, E. R. Plankton and its relationship to chemical factors and environment in White River Canal, Indianapolis, Indiana. Butler Univ. Bot. Stud. **6:** 30–53. My [Je] 1943.

Juday, C. The summer standing crop of plants and animals in four Wisconsin lakes. Trans. Wis. Acad. **34:** 103–133. 1942 [Ap 1943].

Keller, C. O. A comparative study of three Indiana bogs. Butler Univ. Bot. Stud. **6:** 65–80. My [Je] 1943.

Leon, H. Vegetación de las Terrazas de Maisi. Rev. Soc. Geograf. Cuba **2:** 33–49. *f. 1–12.* Ap–Je 1942.

McVaugh, R. The vegetation of the granitic flat-rocks of the southeastern United States. Ecol. Monogr. **13:** 119–165. *f. 1–36.* Ap 1943.

Myers, R. M. The vegetation of Idaho. Denison Univ. Bull. **43**^{5}**:** 32–39. *f. 1.* Ap 1943.

Patterson, P. M. Some ecological observations on bryophytes. Bryologist **46:** 1–13. Mr [10 My] 1943.

Potzger, J. E. Pollen study of five bogs in Price and Sawyer Counties, Wisconsin. Butler Univ. Bot. Stud. **6:** 54–64. My [Je] 1943.

Potzger, J. E. & Friesner, R. C. An ecological survey of Berkey Woods: a remnant of forest primeval in Kosciusko County, Indiana. Butler Univ. Bot. Stud. **6:** 10–16. My [Je] 1943.

Potzger, J. E. & Van Engel, W. A. Study of the rooted aquatic vegetation of Weber Lake, Vilas County, Wisconsin. Trans. Wis. Acad. **34:** 149–166. *f. 1–3.* 1942 [Ap 1943].

Vestal, A. G. Unequal scales for rating species in communities. Am. Jour. Bot. **30:** 305–310. *f. 1.* 25 My 1943.

Welch, W. B. A study of the phytoplankton of Crab Orchard Lake. Trans. Ill. Acad. **35:** 81, 182. *f. 1–3.* D 1942.

GENERAL BOTANY
(including biography)

Asmous, V. C. K. A. Timiriazev (1843–1920), an appreciation. Chron. Bot. **7:** 301, 311. Je 1943.

Bean, R. C. Arthur Herbert Norton. Rhodora **45:** 217–220. Je 1943.

Blaydes, G. W. Staining inulin crystals in plant tissues. Ohio Jour. Sci. **42:** 81, 82. Mr 1943.

Buchholz, J. T. Charles Joseph Chamberlain. Bot. Gaz. **104:** 369–370. *port.* 31 Mr 1943.

House, H. C. Clarence J. Elting and his herbarium. Torreya **42:** 181–190. N–D 1942 [24 Ap 1943].

Johnston, I. M. Publication dates for the botanical parts of the Pacific Railroad reports. Jour. Arnold Arbor. **24**: 237–242. Ap 1943.

Lloyd, F. E. The carnivorous plants. *i–xv*, 1–352. *pl. 1–38* + *f. 1–11*. Chronica Bot. Co., Waltham, Mass., 1943.

McAtee, W. L. Some local names of plants—VIII. Torreya **42**: 153–168. N–D 1942 [24 Ap 1943].

Mason, H. L. Ethel Katherine Crum. Madroño **7**: 33–35. Ap 1943.

Ochoterena, I. Outline of the geographic distribution of plants in Mexico. Chron. Bot. **7**: 311–315. Je 1943.

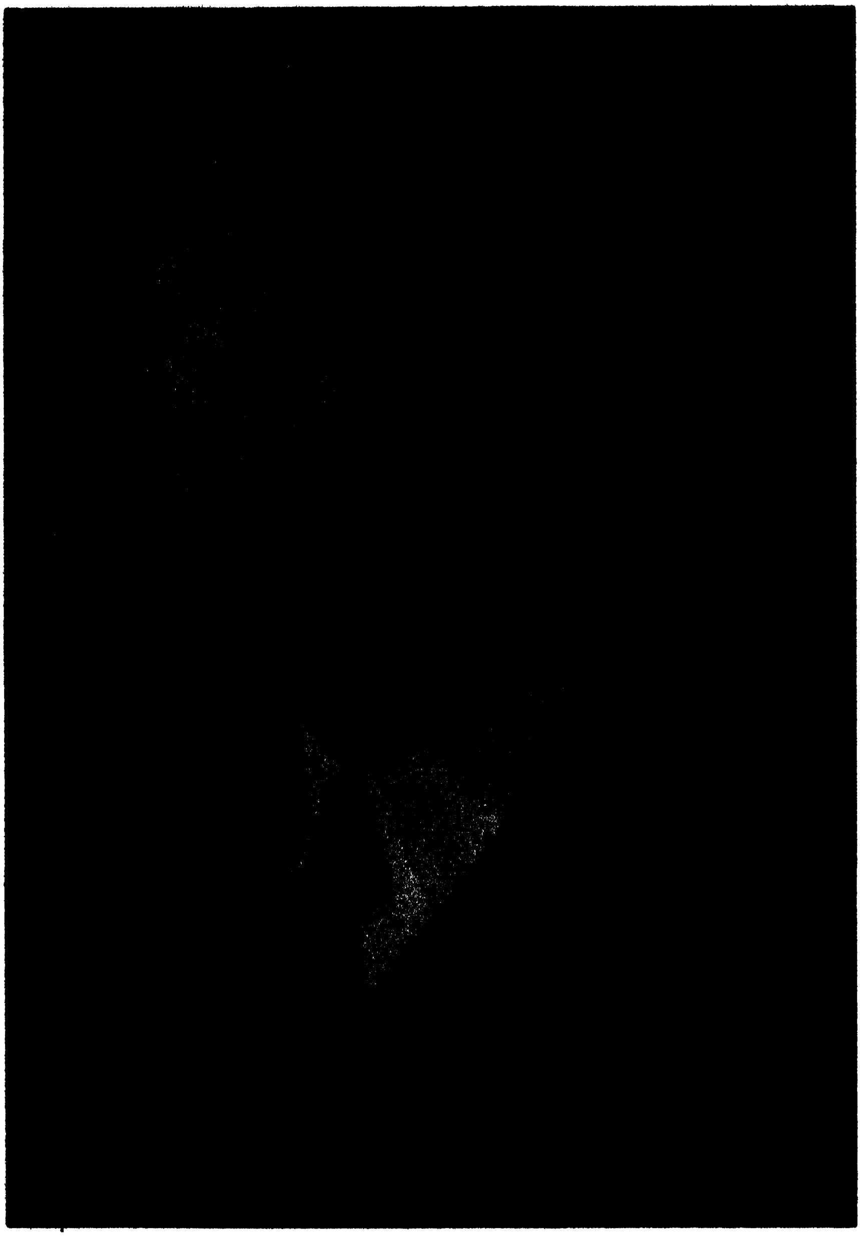
Pennell, F. W. Bontanical collectors of the Philadelphia local area. Bartonia **21**: 38–56. 27 My 1942. **22**: 10–31. 7 My 1943.

Seaver, F. J. William Sturgis Thomas. Mycologia **35**: 133. *port.* 5 Ap 1943.

Standley, P. C. & Steyermark, J. A. The vegetation of Guatemala, a brief review. Chron. Bot. **7**: 315–318. 1943.

Woodworth, R. H. Economic plants of St. John, U. S. Virgin Island. Bot. Mus. Leafl. **11**: 29–56. 22 Ap 1943.

Wulff, E. V. An introduction to historical plant geography. *i–xv*, 1–223. *f. 1–35*. Chronica Botanica, Waltham, Mass., 1943.



TRACY ELLIOT HAZEN

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 559–562 NOVEMBER, 1943

TRACY ELLIOT HAZEN
1874–1943

CORNELIA L. CAREY, HAROLD C. BOLD AND JOHN HENDLEY BARNHART

Professor Tracy Elliot Hazen, distinguished botanist and honorary life member of the Torrey Botanical Club, died March 15, 1943, at Waterbury, Connecticut, after several years of declining health. He was the youngest of seven brothers, three of whom, Rev. Carleton Hazen of Middletown, Connecticut, Rev. William Hazen of Auburndale, Massachusetts and Dr. Robert Hazen of Thomaston, Connecticut, survive him. He was born July 4, 1874, in Jericho Center, Vermont, the son of Rev. Austin Hazen and Mary Jane (Carleton). His early years were spent in the vicinity of his birthplace, where he had ample opportunity to develop his life-long interest in plants.

He prepared for college at the Mount Hermon School, and was graduated from the University of Vermont in 1897 with the A B. degree, Magna Cum Laude He was elected to membership in Phi Beta Kappa at this time. As a student he was keenly interested in the study of the classics, and his decision to devote his major interest to botany was the occasion of disappointment for faculty members of the classical department. In this connection he often recalled the stimulation and encouragement he had received from Professor L. R Jones, at that time in charge of the botanical work at Vermont. The meticulous care and critically keen powers of observation, which are so characteristic of Dr. Hazen's later publications and researches, are already apparent in his senior thesis on *Sphaerella lacustris*, a study which he later elaborated and published as a Memoir of the Torrey Club. The beautifully colored illustrations from this paper have been reproduced in numerous texts. Dr. Hazen remained a loyal son of the University of Vermont, returning frequently to participate in the alumni activities during the annual Commencement week.

During the three years, 1897–1900, he pursued graduate studies in botany and zoology at Columbia University, receiving the A.M. degree in 1899 and the Ph.D. the following year. At the suggestion of Professor L. M. Underwood, he carried on critical taxonomic studies of the filamentous Chlorophyceae. The results of these studies were ultimately published in the eleventh volume of the Memoirs of the Torrey Club. He became an indefatigable collector during this work. During this period he was elected to membership in the Torrey Botanical Club, in the activities of which he maintained an active interest until his death, serving as its president in

The portrait of Doctor Hazen is published with the assistance of the Lucien M. Underwood Memorial Fund.

[THE BULLETIN for September (70: 449–558) was issued September 1, 1942]

1934 and 1935, as associate editor in 1903–1911 and 1932–1939, and as editor in 1924–1931. After forty years of loyal service and annual membership he was elected an Honorary Life Member in 1939.

Dr. Hazen served as Director of the Fairbanks Museum of Natural Science at St. Johnsbury, Vermont, during 1901–1902, continuing his collection and study of the algae, as well as of the ferns and flowering plants. He returned to Columbia as assistant in the Department of Botany from 1902 to 1903. In January of the latter year he was called to Barnard College as Tutor, to continue the work of Miss Louise B. Dunn, who had died. Thus began an association with that school which was to continue for thirty-six years. He attained to the rank of associate professor which he held at the time of his retirement in 1939.

The years at Barnard were exceedingly fruitful in research (much of which remains unpublished), and more especially in teaching. Few others have given so unstintingly, so unselfishly, and with such complete devotion to their students. Professor Hazen was driven by his ideal of providing living specimens in various stages of development for his students; he spared no effort, time or expense in realizing it. In the early years he traveled long distances by bicycle through New York City and its suburbs collecting the necessary material. Later, the excursions were made by public conveyance, always at his own expense. His hundreds of carefully chosen microscopic preparations were personally prepared and greatly enhanced the value of his courses for the student. He had an uncanny ability for transmitting his own extremely keen powers of perception to his students, and was never content until the dullest of the group had correctly observed and understood the most obscure features of the specimen before him. He was unflinchingly zealous in accomplishing this purpose, giving ungrudgingly of his leisure hours to all who sought help. Teaching of this high order is unfortunately all too rare.

His research interests were fundamentally in the Chlorophyceae, more especially the unicellular Volvocales; wherever he traveled he studied, preserved, and prepared notes and illustrations of the local representatives of the group. Many plates of beautifully colored illustrations executed during these studies bring to light a number of species and several genera new to science; it is hoped that these may be published. He was abundantly endowed with the patience, keenness and perseverance necessary for the critical study of these motile organisms. His publications on *Lobomonas* and *Brachiomonas* reflect countless hours of grueling, long-continued microscopic observation, which were rewarded by a completeness of understanding of their structure and reproduction, scarcely equaled by others. His failure to publish much of his work may be attributed to his inordinately high ideals of perfection and thoroughness. In addition to the algae, Professor Hazen

maintained a lively interest in the angiosperms, and in this connection published his well known study of trimorphism in *Pontederia.*

Professor Hazen traveled quite extensively in Europe, South America, and the West Indies, collecting and studying the local floras, and at the same time nurturing his increasing interest in genealogy. He was a member of a botanical expedition to the high Andes of Colombia in 1922, and of Dr. Britton's expeditions to Trinidad in 1920 and to Porto Rico in 1924.

In addition to his duties at Columbia, Professor Hazen taught in the course on algae at the Marine Biological Laboratory, Woods Hole, Massachusetts, during the summers of 1924 and 1926, and served in a similar capacity at the Hopkins Marine Station, Pacific Grove, California, during the summer of 1930.

For a number of years he served as an appointed member of the Board of Managers of the New York Botanical Garden from the Torrey Botanical Club, and was also a member of the Corporation of the Botanical Garden until 1942. He represented the Torrey Botanical Club at the International Botanical Congress in Amsterdam in 1934, at the Centenary Celebration of the Botanical Society of Edinburgh in 1936, and at the meeting of the British Association for the Advancement of Science in 1938. In spite of extreme debility, and against his physician's advice, he attended the celebration of the seventy-fifth anniversary of the Torrey Club in June 1942. This proved to be his last opportunity for active participation in the Club's activities.

After retiring Professor Hazen gave himself more fully to genealogy, and achieved considerable distinction and recognition in this field. He wrote several papers of genealogical interest which were published in the New England Historical and Genealogical Register in 1939 and 1940 as *Contributions for the Tercentenary of Rowley, Massachusetts*, and left a number of other papers in manuscript. In recognition of his scholarship he was invited in 1939 to deliver the main address at the celebration of the Tercentenary of Rowley, Massachusetts

Beside the Torrey Botanical Club Professor Hazen held memberships in a number of other societies, among them the American Association for the Advancement of Science, the Botanical Society of America, the Marine Biological Laboratory, the New England Botanical Club, the Connecticut Botanical Society, the American Fern Society and Sigma Xi. He was also a member of the Vermont Historical Society, the Massachusetts Historical Society, the New England Historic Genealogical Society, the Society of Colonial Wars in Massachusetts, the Society of Mayflower Descendants in Connecticut and the Society of Sons of the American Revolution.

In a letter to Professor Hazen's family the Corresponding Secretary of the Club has aptly summarized the sentiments of its members in writing:

" . . . the Torrey Botanical Club was singularly fortunate in having profited by the sound scholarship, the meticulous labors, the faithful devotion to duty, and the kindness of heart of Professor Tracy E. Hazen. All its members admired him, all respected him as a thorough gentleman, and all who knew him intimately loved him."

The published work of Tracy Elliot Hazen

The life history of *Sphaerella lacustris* (*Haematococcus pluvialis*). Mem. Torrey Club **6:** 211–246. *pl. 86, 87.* 8 My [8 Je] 1899.

The seventh annual winter meeting of the Vermont Botanical Club. Rhodora **4:** 64. 6 Mr 1902.

The Ulothricaceae and Chaetophoraceae of the United States. Mem. Torrey Club. **11:** 135–250. *pl. 20–42.* 20 O [10 S] 1902.

The habitat of the slender cliff-brake. Torreya **2:** 176. 25 N 1902.

Proceedings of the Club: March 8, 1904. Torreya **4:** 73, 74. 13 My 1904.

A new handbook of the genera of freshwater algae. (Review of: West, G. S. A treatise on the British freshwater algae.) Torreya **4:** 154–156. 29 O 1904.

Dryopteris Filix-mas in Vermont. Fern Bull. **14:** 25, 26. Mr 1906.

Oxalis Brittoniae at Pownal. Bull. Vt. Bot. Club **3:** 17, 18. Ap 1908.

Proceedings of the Club: March 10, 1908. Torreya **8:** 82, 83. 29 Ap 1908.

Proceedings of the Club: October 13, 1908. Torreya **8:** 265, 266. 25 N 1908.

Willis's Flowering plants and ferns. (Review of: Willis, J. C. A manual and dictionary of the flowering plants and ferns.) Torreya **9:** 56, 57. 26 Mr 1909.

The trimorphism and insect visitors of *Pontederia.* Mem. Torrey Club **17:** 459–484. *pl. 14, 15; f. 1–12.* 10 Je 1918.

Platymonas subcordiformis (Wille) Hazen, comb. nov. Rhodora **23:** 251, 252. 27 F 1922.

The phylogeny of the genus *Brachiomonas.* Bull. Torrey Club **49:** 75–92. *pl. 3, 4; f. 46–50.* 18 My 1922.

New British and American species of *Lobomonas:* a study in morphogenesis of motile algae. Bull. Torrey Club **49:** 123–140. *pl. 5, 6.* 15 Je 1922.

Flora of Penikese, fifty years after: Algae of fresh water. Rhodora **26:** 211, 212. 5 Ja 1925.

Flora of Penikese, fifty years after: Algae of brackish water. Rhodora **26:** 215. 5 Ja 1925.

Botanizing in the Colombian Andes. Jour. N. Y. Bot. Gard. **26:** 132, 133. (30) Je 1925.

The English ancestry of Edward Carlton of Rowley, Mass. New Engl. Hist. Geneal. Reg. **93:** 3–46. *pl.; chart.* (1) Ja 1939.

The ancestry of Ellen Newton, wife of Edward Carlton of Rowley, Mass. New Engl. Hist. Geneal. Reg. **94:** 3–18. *pl.; f.* (1) Ja 1940.

(With Harold Charles Bold) New motile algae from New Jersey. (Abstract.) Am. Jour. Bot. **26:** Suppl. 25. 4 Ja 1940.

Two founders of Rowley, Mass. New Engl. Hist. Geneal. Reg. **94:** 99–112. *pl.* (1) Ap 1940.

Contributions for the tercentenary of Rowley, Massachusetts. (Ap 1940) This comprises separates of the three genealogical papers of 1939 and 1940, with a general title-page.

BARNARD COLLEGE, COLUMBIA UNIVERSITY, AND
THE NEW YORK BOTANICAL GARDEN
NEW YORK

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 563–598 NOVEMBER, 1943

THE OSMOTIC QUANTITIES OF THE CELLS IN THE HYPOCOTYL OF HELIANTHUS ANNUUS SEEDLINGS[1]

WILLIAM A. BECK AND BASILIA ANDRUS

INTRODUCTION

In recent years great interest has been manifested in the nature of growth in plants by cell enlargement. In particular a source of energy has been sought which would satisfactorily account for the phenomenon of the enlargement of the plant cell. The older notion that turgor is entirely responsible for the enlargement became untenable with the discovery of Ursprung and Blum that the turgor in the growing root cells of *Vicia faba* is minimum in the zone of maximum growth. More recently an active growth of the cell wall was made accountable for the phenomenon. The auxin was made responsible for this growth of the wall, but for some time it was not clear if the auxin caused it directly or only by acting inductively upon the protoplast. Growth of the wall by intussusception can hardly be doubted in view of recently proved facts, and there can be little, if any, doubt that this growth of the wall is due to the addition of materials elaborated by the protoplasm, which is influenced in its activity by the growth-promoting substance. It is probable that the influence of auxin evokes, not only the elaboration of the necessary wall material, but other growth phenomena as well, such as the production of the solutes necessary to maintain the turgor of the growing cells.

It is the purpose of the present study to investigate carefully the active growth of developing cells and their osmotic quantities, with the end in view of correlating these phenomena and drawing such conclusions as are possible regarding changes in the physical nature of the protoplast, the cell sap, and the wall. The results should give a better understanding of the nature of growth by cell enlargement, and of the energies which are involved.

The terms expressing osmotic quantities have been used in such a variety of meanings that one is in doubt many times about their real significance when used by an author who fails to define his terms accurately. For that reason care is taken here to define each term and state its significance. For a review of the literature on this subject the reader is referred to the works of Ursprung (44, 46), Beck (3), and Stark (40).

In plant physiology the term osmotic quantity is employed to designate any of the quantities which refer to such pressures or tensions in the living

[1] The cost of publication of this paper was assisted by the Institutum Divi Thomae, Bradley Hall, Palm Beach, Flórida.

plant cell as depend directly or indirectly upon osmotic phenomena, including components that result from combinations of these elementary vector quantities.

In previous work on growth phenomena and pigment production (6, 7, 9, 10, 12, 13, 14, 15), *Helianthus annuus* was used; it was natural to choose the same object for experimental study in the present work since a body of data regarding these seedlings is on hand. From previous experience and careful propagation each year it was possible to have strictly comparable plants from seeds of the same strain grown under identical conditions.

Ruge (35, 36) studied the hypocotyl of *Helianthus* seedlings in an effort to determine the influence of heteroauxin on cell enlargement, and recorded osmotic quantities determined by him which may well be compared with the data we present here. But it must be remembered that the regions of the hypocotyls which he employed are not the same as in our experiments and he cultured his seedlings somewhat differently. His seedlings were not of the same age or size as ours and he confined his studies to the cortical tissue, while we studied both the epidermal and cortical tissues. The exact determination of the osmotic quantities is tedious and involved; it demands much time, so that conceivably Ruge was obliged to give less attention to this phase of his work, considering the many and varied operations that he was obliged to carry out within a limited time to achieve his objective. He followed Ursprung's methods for the determination of some of his quantities, but it is not clear if he did so for all.

We proposed to give close attention to the exact determination of the osmotic quantities in normally developing cells, that is, from the time the cells cease to proliferate to the mature state. Our work extended over a period of three years.

METHODS

Etiolated *Helianthus* seedlings, 90 hrs. old, grown under controlled conditions (90 per cent relative humidity and 25° C) were employed. At this age the plants were approximately 45 mm. high. From previous work it was concluded that the cells of the hypocotyl proliferate directly below the base of the cotyledons within a distance less than 2 mm. from the base of the cotyledons, and at a distance of 35 mm. the cells were certainly mature. Accordingly the hypocotyl was divided into seven zones, each 5 mm. long as indicated in figure 1, and the osmotic quantities were determined for the cells of each zone.

The methods devised and described by Ursprung (45) were followed in this work. Our results do not refer to individual cells but to sections of specific tissues. Sucrose was used as a plasmolyzing agent, since it is better than any other agent (2, 20, 41, 51). It is well to remember when comparing our

results with those obtained by Ruge (35) that he used dextrose as his agent in some of his studies.

For the determination of cellular dimensions the eyepiece micrometer of

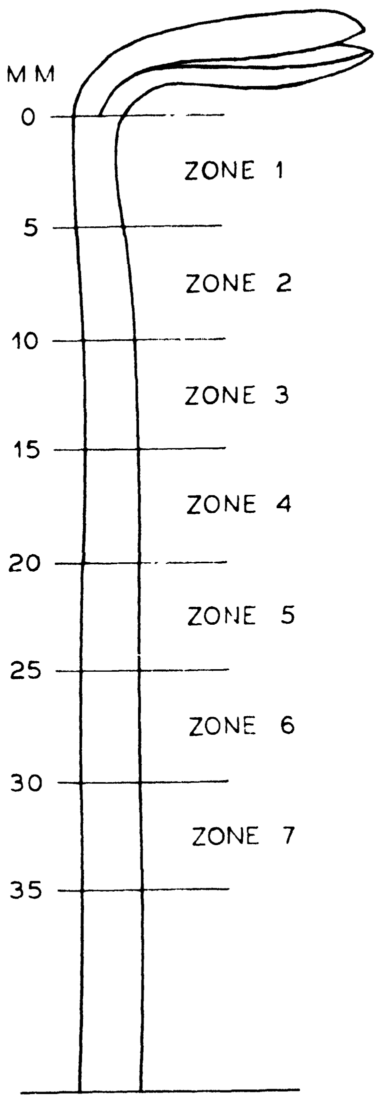


FIG. 1. *Helianthus* seedling as used in the experiments.

the regular microscope was employed, but for the dimensions of sections of tissues and variations of their lengths a special measuring microscope was employed in which the error was not more than ± 0.01 mm.

The order in which the various osmotic quantities were determined was not the same as that followed in the presentation of the work. In the laboratory the order was as follows: first the determination of the sizes of the cells in the normal state, while immersed in paraffin oil; and then the suction tension of the cells by direct measurement; the osmotic value at incipient plasmolysis; and the osmotic value at saturation; together with the respective sizes of the cells in the three states; finally the wall pressure was determined.

For the sake of clarity the data will be presented in the following order: the cellular dimensions and cellular characteristics will be discussed first; and will be followed by the osmotic value of the cell sap in the three states; and the suction tension of the cell as an entity; finally the wall pressure will be discussed.

CELLULAR DIMENSIONS AND CHARACTERISTICS

Discussion of the Cells and Their Walls. Before discussing the osmotic quantities of the cells at different ages it is well to have a clear understanding of the general appearance of the plants which were employed and the sizes and characteristics of the cells at different stages of development.

In figure 1 a diagram of a typical seedling is given. This may well be taken as a diagram of the average form and size of all that were used. Care was taken to draw it exactly to size from a specimen that was considered the average.

The smaller diameter of zone 1 is characteristic. Under the conditions of culture the seedlings were etiolated and the carotene and xanthophyll were chiefly located in the cotyledons and the uppermost region of the hypocotyl. The rest of the hypocotyl is opaloid. No effort was made to determine whether the pigment deteriorated with the enlargement of the cells or whether it was merely masked by the total reflection of light in the intercellular spaces formed in the cortical tissue as the hydrostatic pressure of the cells increased in that tissue. Since it has been suggested that the carotinoid pigments may be a part of the respiratory mechanism it is desirable to investigate the possible correlation of pigment production and cell enlargement. If these pigments affect the auxin activity in the protoplast, cell enlargement may in turn be influenced by the presence or absence of these pigments (8, 9).

It was not considered necessary to study regions which lay further removed from the cotyledons than 35 mm. because beyond 25 mm. the cells may be considered mature, as was shown by Beck and Donnelly (13).

It is important in such studies as we have in hand to recognize the distribution of the growth zones, hence a very careful study of the dimensions of the cells in each of the seven zones was made and the results are recorded in table 1.

The length of the cells was determined with the aid of the eyepiece micrometer. The determinations were made at three points in each zone, the uppermost, the lowermost, and the midregions, and the average of these was recorded in table 1. It was considered sufficient to determine the length of the cells as an expression of their enlargement, since actual measurement proved that the diameter of the cells was almost the same in all seven zones. This is in agreement with the fundamental rule that was first suggested by Czaja (19) and verified by Ruge (35) for the hypocotyl of *Helianthus* seedlings, and was further confirmed by Borgström (17), that the cell walls grow in a polar manner increasing their mass in the lateral walls but not appreciably in the transverse. Since the development of the stomatal complexes distorts the neighboring cells, these regions were avoided. No particular difficulty was experienced in the study of the cortical cells.

The cells directly beneath the cotyledons were compressed in general appearance. This region did not extend much beyond 1 mm. and certainly not beyond 2 mm. This is evidently the zone of cell proliferation, and the region in which auxin is produced. The auxin which is present in the remaining 3 mm. of zone 1, in which the cells have begun to enlarge, is probably the auxin which was formed in the uppermost 2 mm. and is in the process of translocation (12).

Since the cells of zone 1 are possessed of a relatively small cell sap cavity, when it is not entirely lacking, reliable figures regarding osmotic quantities can hardly be expected. Our results are, however, included in the table for the sake of completeness. In an effort to interpret the results it must be borne in mind that the forces refer predominantly to the phenomenon of imbibition in this zone. Plasmolytic methods when applied in very young cells yield more or less doubtful results for another reason; namely, that the undeveloped cell walls lack elasticity and rigidity, so that when they are expanded beyond the limits of elasticity in any operation, they do not readily recede with the protoplast when an attempt is made to plasmolyze the cell. It was for this reason that Overbeck (30) and Oppenheimer (29) criticized Ursprung's method of determining the suction tension. To avoid any similar error we modified Ursprung's strip method. After first determining the suction tension by Ursprung's original method in order to obtain threshold values, we made as many independent sections as we deemed necessary, and immersed them simultaneously in graded solutions above and below the threshold values. Each strip was immersed only once in a solution of specific concentration. The size of each strip was determined before immersion and again after immersion. The solution in which a strip failed to alter its size was evidently in equilibruim with the cells. In this manner the possibility of stretching the walls beyond the limits of elasticity was avoided.

In view of the fact that there is some discussion regarding the manner in which the volume of the cell enlarges, i.e., whether it enlarges by the insertion

of new material or whether only passively by a process of stretching it beyond the limits of elasticity under the stress of the hydrostatic pressure from within, it was thought well to measure the thickness of the cell wall in the different zones. Unfortunately we were not equipped to do this with sufficient exactness, since our instrument error using the eyepiece micrometer was too great. We did, however, make an attempt to get what information we could by this method.

Frey-Wyssling (22), employing the double refraction method, proved that the cellulose chains of the cell walls of grasses shift during certain phases of growth. Ruge (36), employing the same method, concluded from his experiments that such shifting of the chains occurs in *Helianthus* seedlings in a zone about 4 to 5 mm. long directly beneath the cotyledons. Accordingly he holds that in this zone the cell wall is stretched beyond the limits of elasticity by the inner hydrostatic pressure. Our own less exact methods lead to the same conclusions. This conclusion is probably true in the lowermost region of the first zone. The fact that the diameter is less in the first zone than in the rest of the hypocotyl is in agreement with this conclusion. It was evident to us that the walls of the epidermis became thinner as growth proceeded in the first zone. In the older zones the cell wall became thicker progressively. In the cortical tissue it was more difficult to come to a decision, but there were no contradictory data to prevent us from agreeing with Ruge, that in the very young cells not much material is added to the cell wall by the process of intussusception, but at a distance of more than 6 mm. from the base of the cotyledons there is evident growth of the wall by intussusception (36).

The participation of turgor in the process of growth by cell enlargement has long been a subject of discussion. In 1924 Ursprung and Blum (47) pointed out that turgor is least in the region of greatest growth. In our studies we have found that turgor, or its equilibrant the wall pressure, is least in this region, but not least at the point of inflection of the growth curve, that is at a distance of 6.5 mm. from the base of the cotyledons (10, 14). In our studies of wall pressure we have found that the value is least at a distance of 20 mm. from the base of the cotyledons in the epidermis and at a distance of 15 mm. in the cortical tissue (see figure 5).

Contraction and Expansion of the Cells. The contraction of normal cells when plasmolyzed is very interesting. It was determined by direct measurement and the results are recorded in table 1. When the size of the cell at incipient plasmolysis was plotted against the distance from the base of the cotyledons the curves for both tissues were found to be typical growth curves just as was found to be true for the cells in the normal state (10, 14). This is clear evidence that the walls grow actively, since the walls were not thinner in older than in younger cells, and therefore there could not have

been more stretching beyond the limits of elasticity. The per cent contraction is not the same for the two tissues and does not vary from the average so much in the epidermis as it does in the cortical tissue, an evident indication that the nature of the wall is not the same in the two tissues. The epidermis shows least ability to contract in the second zone and greatest ability in the third, fourth, and fifth, and then definitely declines in the sixth and seventh zones (see table 1 and figure 2). The cortical tissue also manifests a low

TABLE 1. *Sizes of Cells in the Normal, Plasmolyzed, and Saturated States.*

Zone	Incipient Plasmolysis				Normal State		Water Saturated			
	Epidermis		Cortical		Epidermis	Cortical	Epidermis		Cortical	
	Length in Microns	Contract. in Percent	Length in Microns	Contract. in Percent	Length in Microns	Length in Microns	Length in Microns	Expansion in Percent	Length in Microns	Expansion in Percent
1	26.1	1.88	47.31	1.639	26.6	48.1	27.8	4.511	53.816	12.095
2	96.0	1.031	79.38	2.601	97.0	81.51	99.0	2.165	90.198	10.660
3	138.6	2.395	108.14	3.360	142.0	111.90	143.3	0.915	125.517	12.169
4	169.8	1.850	142.36	1.950	173.0	145.2	178.8	3.352	161.298	11.087
5	194.0	2.513	165.06	1.040	199.0	166.8	204.0	2.513	180.624	8.289
6	209.0	1.786	185.34	1.260	212.8	187.7	215.0	1.034	192.563	2.591
7	218.4	1.533	207.58	0.683	221 8	208.9	224.3	1.127	216.407	3.594

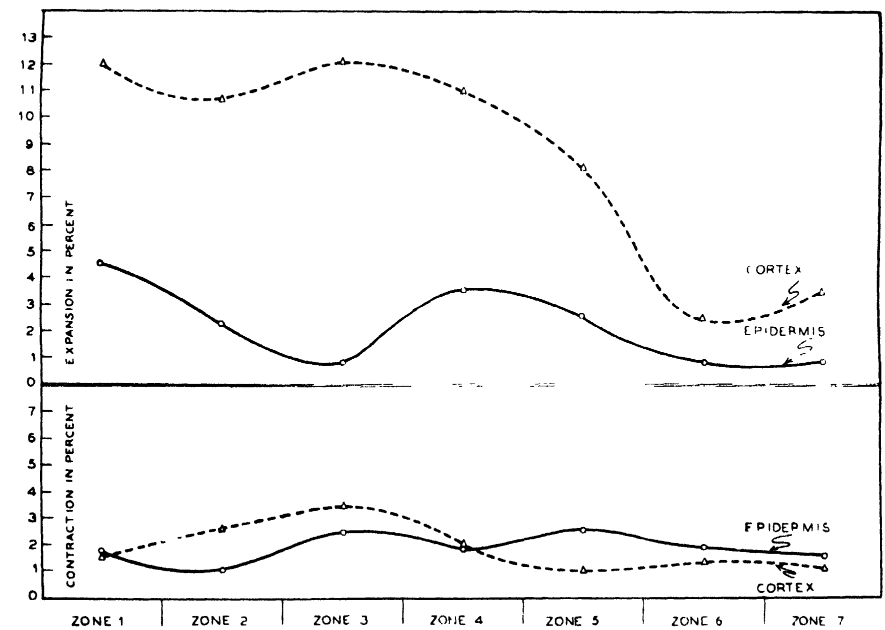


FIG. 2. Variation of the sizes of the cells from the normal, expressed in per cent, at plasmolysis and saturation for the seven zones.

ability to contract in the first zone, but then rises to a maximum in the third, after which there is a steady decline in the older zones where it is lower even than in the epidermis. From this it may be concluded that in the older zones either the cells in their normal state lack water (O_n and O_g being nearly equal might indicate but not prove as much; see table 2) or the walls cannot contract much in the two tissues because of the lack of elasticity. Since the suction tension is relatively low in the older zones there can hardly be a lack of water, so that the low ability to contract must be ascribed to the nature of the wall, i.e. in zones six and seven the epidermis becomes rather rigid, and the cortex becomes more rigid as early as in the fourth zone.

The expansion of normal cells when placed in water was also determined by direct measurement. The cortical tissue shows considerably greater ability to expand than does the epidermis, particularly in the uppermost five zones. This is not difficult to understand from the respective structure and functions of the two tissues.

The ability to expand decreases temporarily in the first three zones and rises to a secondary high in the fourth, and thereafter decreases steadily. In the cortical tissue the ability to expand is unusually high in the first zone and sinks temporarily in the second zone to rise in the third zone to a secondary high, after which it decreases rapidly to the *all* low in the mature cells, almost equal to the low of the epidermal cells. It is interesting that the ability of the epidermis to expand is low in the third zone when it is high in the cortical tissue, which indicates that the development of the cell walls is not identical in the two tissues.

The ability to contract is a safer indication that the wall is elastic than is the ability to expand: if the wall will neither contract nor expand readily it is evident that the walls are rigid. If the walls expand readily, but do not contract readily the indication is that the walls are plastic and that the water supply has not been sufficient to allow further expansion (otherwise they should be stretched beyond the limits of elasticity), either because the water had to be raised in the plant against the force of gravity, or because the potential difference between neighboring suction tensions was not sufficient to allow water to flow readily into the cells. If there is a fair degree of expansion and contraction as well, the indication is that the wall is neither plastic nor rigid, i.e. moderately elastic.

Interpreted in this sense our data show that the epidermis is very plastic in the first two zones, less so in the succeeding ones. In the third zone the contraction is high and the expansion low, accordingly the elasticity is high. The elasticity is maximum in the fourth zone where both contraction and expansion are high. In the more mature epidermal cells both expansion and contraction decrease; that is, the walls are evidently more rigid.

The cortical tissue develops somewhat differently. The degree of contraction is low in the first zone where the extensibility is high, indicating great

plasticity. In the third zone both the expansion and the contraction are high, i.e. maximum elasticity exists. From this point on the expansion as well as the contraction decrease steadily, clearly indicating that the walls are becoming rigid.

From the respective values for the two tissues it is evident that the cortical cells have far less rigid walls than do the epidermal cells, which is as might be expected from a consideration of the respective functions of the two tissues.

It is particularly interesting to study the diagram in figure 1. In agreement with the macroscopic determination of the diameter of the hypocotyl in the first zone, the cells in this zone are always somewhat less in diameter than the cells of the older zones. Only well along in the second zone is the nearly constant diameter attained. If it is assumed that the walls are plastic and that the osmotic turgor develops slowly and the suction tension, nevertheless, remains high, it is evident that the high suction tension is due to the imbibition of the protoplast and is essentially non-osmotic in nature.

Characteristics of the Protoplast. (a) *Gradients.* There is a characteristic gradient of viscosity in the protoplasm of the cell of the hypocotyl of the seedlings, ranging from the zone of cell proliferation to the enlarged, mature cell. We verified this by direct experiment but are not listing our results because they do not show anything more than is already recorded in the literature by Strugger (41) and Ruge (35). There can be no doubt of this fact in the particular case of *Helianthus* seedlings. It appears to be a general fact that young protoplasm is more viscous than older protoplasm, since it was proved in algae and fungi as well as in various organs of the higher plants (18, 26, 34, 49, 50).

It is generally admitted that protoplasm is a complexly built mixture of hydrophilic colloids and we are accordingly justified in applying to it the principles of colloid chemistry. Physico-chemical experiments have shown beyond reasonable doubts that the relative viscosity of a substance is a good indicator of its relative colloidal state. A knowledge of the changes in viscosity of the protoplasm, such as are indicated by the gradient manifested in the developing cells of the sunflower seedlings, aids in a better understanding of changes that occur in the colloidal state of the protoplasm.

The viscosity has been brought into correlation with growth and growth-promoting substances by Strugger (42) employing the hypocotyl of *Helianthus* seedlings, who found that the young cells of the stretching zones require a greater length of time for the protoplast to become rounded off in a plasmolyzing solution than do mature cells, and he concludes that they consequently possess a higher internal non-osmotic pressure expressing itself by a greater viscosity. Ruge (35) obtained similar results. We repeated these experiments and obtained similar results. From the facts recorded in the

literature it is evident that we can express ourselves regarding the characteristics of the protoplasm in the seven zones of our seedlings such as its swelling ability, its stability, and its electrical charge. The swelling power of the protoplasm is considerable in the first zone and negligible in the others; there is a definite gradient from the younger cells to the older ones which is termed the plasmolytic gradient. This must, of course, be borne in mind when interpreting our results, since no effort was made to distinguish between the suction tension which is produced by the suction tension of the cell sap (due to osmosis) and that produced by the suction tension of the protoplasm (due to imbibition). Bennet-Clark, Greenwood, and Barker (16) considered it possible that active "secretion" of water takes place from the protoplast into the cell sap cavity, but it would hardly be justified to consider the increment of water in the cell sap cavity as a kind of synaeresis, since there is active production of solutes as the cells grow older (10, 14). No doubt, the cell sap concentration must bear some relation to the viscosity and the colloidal state of the protoplast, so that the protoplasm is constantly in dynamic equilibrium with its aqueous environment.

Pfeiffer (31, 32, 33) proved that a definite degree of viscosity in the cytoplasm is correlated with a definite electrical charge of the plasma colloid. When the electrical charge is changed then also an electro-viscosity effect must follow. The growing and non-growing cells are accordingly characterized by this, that the variations of the plasma ampholytes from the isoelectric point (I.E.P.) are different. The mature cells are "fixed."[2] There is sufficient experimental evidence in the literature regarding the cH gradients in relation to the differentiation of tissues to warrant the employment of the "plasmatic gradients" as visible expressions of the cH gradients which proceed in the same direction (24, 25, 37, 38).

The established cH gradient is significant for another reason, namely that it suggests a correlation of growth by cell proliferation and cell enlargement. It is well established that there is a difference of electrical potential between the chromatin of the nucleus and the cytoplasm; the nucleus being electro-negative and the cytoplasm electro-positive. Since cell proliferation, which is known to be rhythmic, ceases in the hypocotyl a short distance from the base of the cotyledons, and cell enlargement occurs in a graded manner parallel with the viscosity and the cH gradient, and is also rhythmic, the whole process of cell enlargement, which is known to be induced by natural auxins and heteroauxins (which are characteristically acid in reaction) must be related. It is extremely difficult to consider the function of the chromatin

[2] Because of the ampholyte nature of the protoplast a critical point must be reached at a very definite hydrogen ion concentration, in which the number of anions and cations is the same in their minimum. At the isoelectric point their cH is zero, in which therefore the electrical charge of the colloid is zero, and the number of neutral particles is maximum (cH = O at I.E.P.).

from a purely material concept basis without involving orientating forces, directed outward from bio-molecular electro-magnetic fields.

(b) *Discussion of the Characteristics.* There can be no doubt about the generation of auxin in the zone of cell proliferation. The manner in which it acts to cause cell enlargement and its translocation are not very clear. How gravity influences the auxin is particularly obscure; if it occurs in the form of pure solution gravity cannot affect it, and if it is not in pure solution its translocation by diffusion becomes impossible. These facts suggest that the auxin exercises its influence in a manner comparable to that of "evocators" (27)

Auxin must definitely be regarded as a phytohormone and consequently specificity, such as is attributed to bio-regulators in general, must characterize it. One of the outstanding marks of protoplasm is its specific ability to synthesize asymmetric compounds in which the atoms of the molecules are arranged in a specific asymmetry that cannot be duplicated in inorganic systems. Asymmetry points to a labile, dynamic, spatial arrangement of the atoms in the molecule, and the aging of cells may be regarded as a trend towards stable equilibrium within the bio-molecules. The more unstable the molecule, the greater the free energy content. The forces exercised by highly labile asymmetric molecules of the young proliferating cells directly beneath the cotyledons, through their asymmetry-inducing energy upon other molecules, may be assumed to play a very important role in influencing the growth of the older cells by cell enlargement, the material expression of this would be the formation of auxin.

Science has traveled far since Van't Hoff and LeBel laid the foundations for the science of stereo-chemistry. The valence in a material is no longer considered in a mechanical manner, but is linked to its configuration of electrons and its system of waves. The phenomena attending the asymmetric organic molecule are far more readily interpreted by means of the energy concepts of modern atomic theories than by means of the older theories of the classical physicists. The eH gradient suggests that the "trigger energy" which directs the process of cell enlargement, resides in the chromatin and that it is maximum in the young cells and minimum in the mature cells. It is particularly significant in consideration of this possibility that auxin is acid in reaction. When the cells are too far removed from the source of auxin and the electrical potential difference between the nucleus and the cytoplasm of mature cells is small, and the "trigger energy" is spent, a state of equilibrium is produced, so that the activity of the cell is nearly purely physical and the osmotic quantities are more involved in the functioning of older cells than in the younger.

These notions are helpful to a better understanding of the evident correlation of cell proliferation and cell enlargement, the evident dependence of

both on mitosis, and the influence of the chromatin on the phenomena accompanying growth. They also help to make it clear that the nucleus is indispensable for the physiological activity of the cell in general, and growth by cell enlargement in particular. It is suggested accordingly that the natural auxin has its source in the nucleic acids and depends on the mitotic activity for its production. Also that its bio-regulating effect depends upon its power to direct the formation of specific asymmetric structures within the protoplasm and that this effect is inductive and need not necessarily be conducted to exercise its influence. The induction might well occur electro-magnetically. This view receives encouragement from the fact that so many different kinds of organic acids can exercise an effect similar to that of auxin upon plant cells. It is doubtful if these acid agents produce exactly the same physiological effect as does the natural auxin, but their acid nature can influence the protoplasm in such a manner that growth by cell enlargement is simulated.

THE OSMOTIC VALUE AND THE EQUIVALENT SUCTION TENSION OF THE CELL SAP OF CELLS IN THE NORMAL, PLASMOLYZED, AND SATURATED STATES

The concentration of the sap, which contains organic and inorganic solutes, is not the same for a given cell in the normal, plasmolyzed, and saturated states. The concentrations in the three states are symbolized by (O_n), (O_g), and (O_s), respectively, and are expressed numerically in function of the concentration of the plasmolyte which has the same osmotic pressure. The suction tensions which are equivalent to the concentrations (O_n), (O_g), and (O_s) are symbolized by (Si_n), (Si_g), and (Si_s), respectively, and are expressed in atmospheres.

It is evident from the nature of the process employed that for a given cell or tissue:

$$O_g > O_n > O_s; \text{ and}$$
$$Si_g > Si_n > Si_s.$$

This fact is well illustrated by our recorded results (see table 2).

Weber (51, 52) pointed out that the normal permeability of the protoplasm is changed by plasmolysis when certain plasmolytes are employed. He speaks of "plasmolysis permeability." He and Strugger (42) agree with Beck (2) that when sucrose is employed as a plasmolyzing agent there is no immediate influence exerted upon the permeability of the protoplasm. Our experience in the present work is in accord with this view.

The time necessary to produce incipient plasmolysis was found to be greater for young cells than for older cells. This became particularly evident when, after a number of trials, the concentration which produced incipient plasmolysis was determined, and then fresh tissue was placed in the sugar solution of that concentration, which was approximately the correct O_g

value, and the time required to produce plasmolysis was determined. We did not go into this matter as thoroughly as others, but we can safely state that young cells required more time to become plasmolyzed than did mature cells. When excessively high concentrations were employed, the protoplasts of the young cells became plasmolyzed in a shorter time than in the nearly correct O_g concentration, but the form of the plasmolyzed protoplasts was not convex, as it normally should have been. If sufficient time was allowed, however, the "cramped plasmolysis" form, as Weber calls it, changed to the normal convex form. This fact indicates that the protoplast of young cells is more viscous than that of mature cells. It is also evidence that the protoplasm of young developing cells is in intimate union with the cell wall and in the process of plasmolysis is torn away violently at many points, but remains

TABLE 2. *The Concentration and the Suction Tension of the Cell Sap in the Normal, Plasmolyzed, and Saturated States, Expressed in Mols and Atmos., Respectively.*

Zone	At Incipient Plasmolysis				In the Normal State				In the Saturated State			
	Epidermis		Cortex		Epidermis		Cortex		Epidermis		Cortex	
	O_g	Si_g	O_g	Si_g	O_n	Si_n	O_n	Si_n	O_s	Si_s	O_s	Si_s
1	0.28	7.6	0.407	11.41	0.27	7.3	0.405	11.35	0.268	7.24	0.362	10.06
2	0.255	6.8	0.40	11.20	0.248	6.64	0.398	11.14	0.233	6.29	0.360	10.00
3	0.25	6.7	0.385	10.75	0.243	6.49	0.384	10.72	0.241	6.43	0.342	9.46
4	0.24	6.4	0.345	9.55	0.288	6.14	0.344	9.52	0.226	6.08	0.309	8.47
5	0.23	6.2	0.340	9.40	0.225	6.05	0.339	9.37	0.221	5.93	0.312	8.56
6	0.23	6.2	0.310	8.50	0.266	6.08	0.309	8.47	0.214	6.02	0.302	8.26
7	0.23	6.2	0.295	8.05	0.266	6.08	0.294	8.02	0.225	6.05	0.284	7.72

attached at some points. These facts suggest that in careful work in which the plasmolytic method is employed, the final readings should be determined with solutions which are not far removed from the true O_g concentration, and sufficient length of time should be allowed for evident convex plasmolysis These precautions were taken in our work, and we feel certain that the protoplast was not injured as the result of violent treatment. We found that mature cells usually did not require more than ten minutes to plasmolyze but young cells sometimes required thirty minutes.

Since, as was previously described, the volumes of the cells at incipient plasmolysis, in the normal state, and in the saturated state are known, it is not difficult to calculate the concentrations of the sap in the normal and saturated states from the concentration in the state of incipient plasmolysis by the methods described by Ursprung (45). The equivalent suction tensions can be obtained from the table of Ursprung (45) in which the equivalent concentrations and osmotic pressures are listed for sucrose. The results which we obtained are given in table 2.

The Osmotic Value at Incipient Plasmolysis. This quantity expresses the concentration of the sap when the protoplast has slightly receded from

the cell wall in consequence of the contraction produced in it by exosmosis after having been placed in a hypertonic sugar solution. When the value is expressed for a tissue it is understood that fifty per cent of the cells are in the state of incipient plasmolysis.

Normally the semipermeable protoplast is in contact with the cell wall, which is permeable. When the protoplast is distended by the hydrostatic pressure within, it usually presses against the cell wall with sufficient force to distend the cell wall, providing the wall is not too rigid. If the internal pressure is relieved, not only does the protoplast contract but also the distended wall. Evidently a rigid wall will not contract, nor will a plastic wall which is devoid of all elasticity. An elastic wall will contract to a degree commensurate with its degree of elasticity. From these considerations it becomes clear at once that the capacity of the mature cell does not differ much from its capacity in the state of plasmolysis if the wall is rigid because the protoplast leaves the wall as soon as it begins to contract. The plastic walls of young cells, such as those in the first and second zones of our plants, do not recede much because they lack elasticity. It follows that cells with elastic walls manifest a greater difference between O_n and O_g than do cells with rigid walls or such cells that have plastic walls which are readily stretched beyond the limits of elasticity. Even though the value $O_g - O_n$ can give some indication of the nature of the wall, an exact expression cannot be expected because the capacities of the normal cells in the different zones are not comparable. Our O_g and O_n data approximately indicate that both the epidermis and the cortical tissues are most elastic in the third and fourth zones.

In our present study the osmotic value at incipient plasmolysis is of little value in determining the physiological effects of growth in the various zones because of the excessive number of variables which are involved; this fact makes comparisons practically impossible. This does not, of course, mean that in general, all other things being equal, the O_g variations cannot serve as indicators of the variation in the physiological activity of the protoplast in response to external factors. As Beck (4, 5) showed, the O_g is appreciably affected by certain external factors which indicate a physiological reaction in the protoplast.

The values which we obtained for the cortical tissue are consistently lower than those given by Ruge for the same tissue. The lack of light and relatively high humidity conditions which prevailed constantly in our experiments (but not in Ruge's) tend to lower the O_g, so that the order of our data is as might be expected.

Beck (5) showed that the tissues of herbaceous plants have lower O_g values than do woody plants. The relatively low values which we obtained in the present experiments are in accord with this fact. The average values,

0.244 mol. for the epidermis and 0.354 mol. in the cortical region, are just what might be expected in tender sunflower seedlings grown under the given conditions.

O_g for the epidermis in zone 1 (0.28 mol.) is high compared with the value for zone 2 (0.25 mol.). Many trials gave this high value consistently. The embryonic state of many of the cells of zone 1 account for this. In this zone the youngest cells plasmolyze with difficulty because the cell sap cavity is small and the water uptake in the embryonic and slightly developed cells is mostly due to the imbibition of the protoplasm itself.

When an attempt is made to plasmolyze very young cells a plasmolyte of relatively high osmotic pressure must be employed to overcome the imbibition of the protoplasm so that the value obtained for zone 1, which is an average expression for the entire zone, includes the results obtained with embryonic cells which cannot have a true osmotic value and young cells having a small vacuole in which the protoplasm still has a high degree of imbibition.[3] Thus it is clear that the value (0.28 mol.) which was obtained by the methods which are legitimate for older cells, but not entirely reliable for very young cells, is naturally relatively high but involves forces that are non-osmotic in nature. The same may be said for the cortical cells in which the O_g for zone 1 was 0.407 mol.

The O_g gradient in both the epidermal and cortical tissue is in the direction of the movement of the water in the plant. The difference between the values of the oldest and youngest cortical cells is greater than the difference for the corresponding epidermal cells (see table 2 and figure 3). It may be thought that gradients similar to the one found in our seedlings must necessarily exist in all plants. It is, however, a fact that many authors give data for various kinds of plants, where the O_g gradient is not in the direction of the streaming of the water in the plant. The data as given by them are, no doubt, correct and not difficult to understand when it is remembered that it is not the O_g gradient which decides the direction in which the water shall flow, but the gradient of the suction tension of the cell (Sz_n).

It must, furthermore, be remembered that it is not to be concluded from the data given in table 2 that the O_g of the older tissues is low because the normal influx of water was greater than the amount of solute which was produced during the process of cell development, because Beck (10) showed that in epidermal cells of strictly comparable plants the production of solute is directly proportional to the growth of the cells. Beck, Lonsing, and Andrus (14) showed, in strictly comparable plants, that this is also true for the cortical cells. It follows that the lower O_g value in the older cells cannot be ascribed to a lack of the production of solutes, but must rather be ascribed

[3] In this connection the experience of Weber (52) and Strugger (42) should be recalled. They proved that the viscosity and imbibition pressure is maximum in the youngest cells and decreases as the cells develop.

to the increased capacity of the older cells and the changed conditions of the cell wall, particularly its increased rigidity.

Beck (5) showed in tests which he made on many plants that the O_g of the epidermis is always lower than the O_g of tissues that lie within. Our figures are in accord with this fact. The difference between the O_g values found for the cortical and epidermal tissues is greater in young zones than in mature zones (see figure 3). These results indicate that in general the

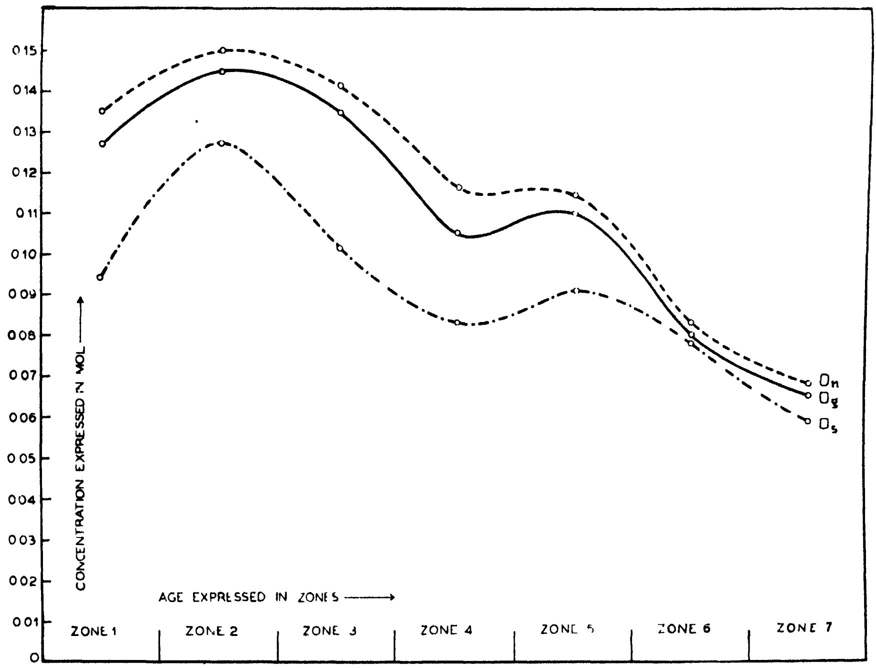


FIG. 3. Difference between the epidermal and cortical sap concentrations: O_g, O_n, O_s, correlated with the age of the tissues.

cortical cells can change their volume considerably more than the epidermal cells can during the process of plasmolysis, at least in the first five zones. This would indicate that the cortical tissue is a more dynamic tissue than is the epidermis. No doubt, the fact that relatively more solute is produced in the cortical tissue than is produced in the epidermis, is also a factor which must be borne in mind in comparing the O_g values for the two tissues. As a matter of fact the thickness of the wall is greater in the older epidermal cells than it is in the older cortical cells. In this connection it is interesting to note that in zone 3 the hypocotyl takes on an opalescent appearance, while in zones 1 and 2 the general appearance is more waxlike. The opalescence is, no doubt, the result of the total reflection of light caused by the intercellular spaces of the cortical tissue that are formed, as the result of the hydrostatic

pressure of the individual, cylindrical cortical cells, which are only in tangential contact. This may be taken as an indication of the dynamism of the cortical tissue.

Concentration of the Normal Cell Sap (O_n). This quantity expresses the concentration of the cell sap as it actually occurs in the plant at the time when the tests are made. It is symbolized by O_n and is expressed in molar concentration. It must not be confused with the osmotic value at incipient plasmolysis. This value can change rapidly in response to external factors without necessarily suffering a change in the amount of solute which is present. In the particular experiments under consideration such fluctuation in response to external factors did not occur, because all the plants employed were strictly comparable and the external factors which might influence the concentration of the sap were carefully controlled and were approximately constant. The results obtained are in table 2.

The suction tension of the contents of the cell in the normal state (Si_n) expresses the negative physical pressure which is caused by the osmotic virtue of the solutes contained in the cell sap. Like all other suction tensions it is expressed in atmospheres. The equivalent concentration is the osmotic value of the sap in the normal state, and is expressed in mols; it is symbolized by O_n. Since both the concentration and the suction tension of the sap in the normal state are useful in the comparisons and discussions for the seven zones of the hypocotyl of *Helianthus* seedlings they have been arranged in table 3.

TABLE 3. *Suction Tension* (Si_n) *and Equivalent Concentration of the Cell Sap* (O_n) *in the Normal State for Helianthus Seedlings.*

Zone	Epidermis		Cortical		Tab. Diff. of (Si_n)
	(Si_n) in Atmospheres	(O_n) in Mol.	(Si_n) in Atmospheres	(O_n) in Mol.	
1	7.3	0.270	11.35	0.405	4.05
2	6.64	0.248	11.14	0.398	4.50
3	6.49	0.243	10.72	0.384	4.23
4	6.14	0.228	9.52	0.344	3.38
5	6.05	0.225	9.37	0.339	3.32
6	6.08	0.226	8.47	0.309	2.39
7	6.08	0.226	8.02	0.294	1.94

The normal suction tension of the cell as an entity (Sz_n) is not given by the value Si_n because the wall pressure, and possibly some other vectors, tend to prevent an influx of water into the cell induced by the vector Si_n. Si_n and Sz_n differ in scalar value but not in direction. The two quantities usually vary in the same way.

The suction tension of the normal cell sap and the hydrostatic pressure produced by the influx of water into the cell sap cavity affect the state of the

protoplasm. It is well known that the protoplasm of aging animal tissues loses water just as do hydrophilic colloids. In gels the time factor is especially apparent. It cannot be concluded from this, however, that the cell sap of developing plant cells is the result of the aging of the protoplasm in these cells. The protoplasm of aging animal tissues increases in viscosity, but in the protoplasm of plant cells, which grow by cell enlargement, the viscosity decreases. For a review of the literature on this subject the reader is referred to Strugger (42). Strugger proved conclusively and gave experimental evidence that the plasmatic characteristics are distributed in a regular manner in the form of a plasmatic gradient in leaves, roots, and shoots, and that these characteristics can be immediately correlated with the physiological zoning. The plasmatic differences of the cells in the process of enlargement consists in the significantly higher degree of viscosity of the protoplasm in the growing cells in comparison with viscosity of that of the mature cells (42; see also Weber, 48).

The production of solute must be regarded as an active physiological process concomitant with other growth phenomena induced by auxin. Beck (10) and Beck, Lonsing, and Andrus (14) showed that in developing cells of the hypocotyl of *Helianthus* seedlings the production of solute in growing cells is proportional to the growth.

These findings indicate that the water which is available for the active protoplasm is of great importance for its optimum physiological activity. The amount of water which may be withdrawn from the protoplasm without serious injury is limited. An excessive supply of water, which may be regarded as waterlogging, is not favorable for the physiological activity of the protoplasm, as was shown by Beck (11). The O_n represents the concentration of the cell sap which is in equilibrium with the active normal protoplasm.

It follows from these considerations that a knowledge of the O_n should prove to be valuable, not only for our present purpose, but also for future comparisons and studies regarding the physiological activity of developing cells.

Rapid variations of the O_n may not, however, be taken as indicators of physiological activities because changes in O_n due to external factors occur very quickly and are largely due to purely physical forces. In our experiments there were no such rapid changes either in the O_n or in the factors of the environment.

Many of the data given in the literature for O_n (sometimes confused with the quantity O_g) were obtained by cryoscopic methods. Such data must be recorded as average values for tissue complexes, organs, or entire plants, and are of little value in discussions regarding changes in the cells during their development. The data of Ursprung and Blum and of others who followed their lead in the study of osmotic quantities give Si_n values for individual

cells and averages for tissues obtained by calculation from direct plasmolytic determinations. These data are better adapted for comparative studies. Our data, given in table 3, express the average value for the cortical and epidermal tissues in the respective zones as indicated. Since they were obtained by the plasmolytic methods according to the direction of Ursprung and Blum, and since the factors of the environment were controlled and all plants were strictly comparable, they can serve to indicate changes in the state of the growing tissues.

The values for O_n given in table 3 are relatively low when compared with values of similar tissues given in the literature for mature plants. This is not surprising because the young seedlings were grown in light sandy, moist, soil, and in air of high relative humidity at optimum temperature. It is well known that external factors in general influence the O_n and the Si_n. Air of low relative humidity, dry soils, and temperatures varying greatly from 25° C tend to increase these quantities (4, 44).

There is an almost regular but not sharp gradient extending from the oldest cells in the seventh zone to the youngest in the first zone of the epidermis. A similar, but even sharper gradient is evident in the cortical tissue. The Si_n gradients are, of course, similar to the O_n gradients and the numerical expression of the quantity in atmospheres makes the gradient more pronounced (7.3–6.08 atmos. and 11.35–8.02 atmos. respectively; see table 3). It cannot be concluded legitimately that such O_n gradients in the flow of water in the plant must necessarily exist because it is not the quantity Si_n but rather the quantity Sz_n which decides in which direction the water will flow.

The values of Si_n and O_n are consistently higher in the cortical tissue than they are in the epidermal tissue. The differences are given in the last column of table 3 (see also figure 3). These differences show clearly that there is an Si_n gradient and an O_n gradient radially from the epidermis to the cortical tissue. These gradients must not be regarded as proofs that the water will necessarily move from the epidermis to the cortical tissue, since the Si_n and O_n differences are not satisfactory indicators of a difference of potential between any two cells or tissues. As stated above, it is the Sz_n gradient which is the deciding factor for the direction of the flow of water. Other things being equal, however, the gradient as we find it favors a similar gradient for the suction tension of the cell Sz_n and tends to cause a flow of water from the epidermis to the cortical tissue. These findings, therefore, are in harmony with the view that the epidermis tends to serve as a water reservoir. In general the values obtained favor the notion that the water flows upward in both tissues and inward from the epidermis to the cortex. The difference between the suction tension of the sap of the two tissues is considerably greater in the youngest zone (zone 1) than it is in the oldest zone (zone 7); 4.05 atmos.–1.94 atmos (see table 3). This great difference does not

imply that the difference is equally great for the suction tension of the two tissues. Later, attention will be drawn to the fact that the figures for the suction tension of the sap and the suction tension of the tissues are of the same order, but not of the same magnitude, and that the difference between the suction tension of the cortical tissues and the epidermal tissues of the youngest zones and of the oldest zones is actually considerably less (5.8 atmos.–4.2 atmos.; see table 4) than it is in the present case for the suction tensions of the sap in the same tissues. This indicates that the wall pressure in these two zones has changed considerably in the process of growth.

The Concentration of the Sap When the Cell is Saturated with Water (O_s). This quantity expresses the concentration of the sap when the cell has been permitted to take in all the water possible, while being immersed in water. It is symbolized by O_s and is expressed in molar concentration.

A considerable difference between O_n and O_s would indicate that much water can be absorbed by the normal cell when thus immersed, i.e. the suction tension of the cell is not rapidly reduced by the influx of water, or in other words a counter-pressure is not rapidly set up during the influx of water. From this it follows that under such conditions the cell wall does not develop an appreciable wall pressure as the result of expansion by the hydrostatic pressure.

When the difference ($O_n - O_s$) is not great it may be because the capacities of the cells are large and the plant in the normal state can take up water without considerable reduction of the concentration of the cell sap. In the present experiments the difference is small and the conditions are such that both tissues in the normal state are almost saturated. One may not use the difference $O_n - O_s$ as a basis of judgment regarding the elasticity of the cell walls without risk of error.

The results indicate that both the cortical and epidermal tissues are more plastic in the first and second zones and more rigid in the sixth and seventh.

The differences between the concentrations of the sap in all three states becomes less with age. In the mature zones the differences between the concentrations for the sap in the two tissues in the three states are all nearly the same (see figure 3). This is, no doubt, due to the increased rigidity of the wall in both tissues. These differences of concentration in the two tissues are always least for the O_s and greatest for the O_n.

It should be remarked here that the value Si_s is numerically equal to the wall pressure W_s, since the action and reaction are equal and opposite in direction when the gorged cell is in a state of equilibrium and the wall pressure upon the protoplast and vacuome prevents the further influx of water.

SUCTION TENSION OF THE CELL IN THE NORMAL STATE (Sz_n)

Since the suction tension of the cell, as an entity (Sz_n), is the result of the suction tension of the contents of the cell (a vector acting in one direc-

tion) and the wall pressure (an antagonistic vector), important conclusions regarding the nature of the wall in growing regions can be arrived at from a knowledge of this osmotic quantity for cells in various phases of growth. Physical changes in the growing cell wall produce definite effects upon the force which tends to cause water to flow into a cell, even though the wall itself is pervious to water and does not prevent the water system from being continuous from one cell sap cavity to another, through the membranes and the protoplasm itself.

This quantity (Sz_n) expresses the force per unit area with which the cell as a whole tends to draw water into itself, either from a direct source of water or from some neighboring cell which has less tension. It is not our purpose to determine at this time whether the cell is active or passive in this process of water intake, but merely to determine the vector value which tends to produce a state of equilibrium.

The numerical expression of this quantity (Sz_n) is a good indicator of the tendency of water to flow in one or the other direction: from the environmental cells to a given cell or in the reverse direction. In the present study we are not considering the suction tension of individual cells but the average Sz_n of the cell complex in a section of a given tissue as determined by the simplified method of Ursprung (45). This average value will indicate the general direction of the flow of water.

The numerical expression of this quantity can be determined directly and can also be calculated from the known osmotic pressure of the normal cell sap which is numerically identical with the suction tension of the sap in the normal state, and the known wall pressure which tends to press water from the cell, according to the law of Ursprung as expressed in the equation:

$$Sz_n = Si_n - W_n \qquad (1)$$

in which Sz_n is the suction tension of the cell; Si_n, the suction tension of the contents of the cell; and W_n, the wall pressure.[1]

In the present work the values for the epidermal and cortical tissues in various zones of the hypocotyl of *Helianthus* seedlings were determined

[1] Here no account is taken of vectors other than that of the wall pressure which tends to reduce the suction tension of the cell, such as the tension or pressure of neighboring tissues. The complete equation is:

$$Sz_n = Si_n - (W \pm A) \qquad (2)$$

in which A represents the additional forces such as tissue tension, besides the wall pressure which tends to increase or decrease the suction tension of the cell.

It would, of course, have been most desirable to have determined the term A, particularly for the pressure produced by the epidermal tissue upon the cortical in the normal hypocotyl, but we were unable to devise a method to do so. In the interpretation of the results this must be borne in mind that our results refer to the suction tension of an excised group of cells in which the counter pressure of the epidermis upon the cortical tissue was necessarily disregarded. In spite of the difficulty of not being able to obtain more than an approximation of the suction tension of the cells in the normal state, the data are very enlightening.

directly and also by calculation, and the results have been recorded in table 4. The symbol Sz_n is employed to express this average value of the tissue even though it strictly refers to individual cells. In order to determine the suction tension directly by experiments some authors keep the same test strip and place it in different concentrations of the plasmolyte and note in which concentration the strip maintains its original length. The osmotic pressure of that concentration is accepted as the suction tension of the sample. This method is satisfactory if the wall is elastic and is not stretched beyond the limits of elasticity. Since we have evidence that the walls of young cells of the hypocotyl in question are not elastic but plastic, it was not safe to employ this method. We therefore never carried a test strip from one concentration to another. A fresh sample was taken for every concentration employed. After preliminary tests indicated the upper and lower limits of the Sz_n value, with but slight variation, final tests were made in graded solutions, which did not vary much from each other and were within the limits found in the preliminary tests. The osmotic pressure of the concentration, in which the sizes of the cells did not vary from the original, was accepted as the Sz_n of the cells tested.

TABLE 4. *Suction Tension of the Cells (Sz_n) in the Epidermal and Cortical Tissues of Helianthus Seedlings.*

Zone	(Sz_n) in Atmospheres				Diff. of (Sz_n) of the Tissues	
	Epidermis		Cortical			
	Exp. Data	Cal. Data	Exp. Data	Cal. Data	Exp. Data	Cal. Data
1	5.3	5.17	11.115	11.093	5.815	5.923
2	5.2	5.24	10.930	10.796	5.730	5.556
3	5.1	5.17	10.600	10.583	5.100	5.413
4	4.9	5.02	9.40	9.265	4.50	4.235
5	4.0	3.92	8.95	9.015	4.95	5.095
6	3.7	3.80	8.20	8.30	4.50	4.50
7	3.4	3.68	7.60	7.630	4.20	3.95

An Sz_n gradient in the direction of the flow of water in a plant, as for example from the roots to the leaves, was long suspected and was finally proven to exist by Ursprung and Blum (43, 44, 47) and others. A study of the nature of the suction tension of the cells makes it evident that such a gradient must exist. If there was ever any doubt about it because of data obtained by cryoscopic methods, it is the result of confusing the quantities, suction tension of the contents of the cell (Si_n), which is numerically identical with the osmotic pressure of the normal cell sap, and the suction tension of the cell (Sz_n). An Si_n gradient in the direction of the flow of water in the plant may exist in a given instance as in our present experiments (see table

3) but in general need not exist. An Sz_n gradient from the oldest cells to the youngest in both tissues is evident and not surprising.[5]

In the epidermis the greatest variation from the average potential difference is between zones 4 and 5 (0.9 atmos.). The greatest variation from the average potential difference in the cortical tissue occurs between zones 3 and 4, namely 1.2 atmos. These greater differences must be interpreted to mean that either critical changes in the nature of the cell walls occur in the hypocotyl between 15 mm. and 25 mm. from the base of the cotyledons, or changes in solute production, or both. Apparently the changes occur somewhat earlier in the cortical tissue (third and fourth zones) than in the epidermis (from the fourth to the fifth zone). Since the amount of solute production is proportional to the growth in both tissues (10, 14), it follows that the high potential difference must be due to changes in the wall, rather than to irregular solute production; and since the enlargement of cells is regular, these relatively sudden changes in suction tension can only be interpreted as due to changes in the wall pressure, and consequently changes in the nature of the wall.

The difference between the suction tension of the epidermal and cortical tissues is considerable, the average being approximately 5 atmospheres. It is somewhat greater than the average in the youngest three zones and somewhat less in the oldest four zones. If the physical pressure imposed upon the cortical tissue is disregarded, these figures would indicate that the water tends to flow from the epidermis to the cortical tissue, which is in harmony with the notion that the epidermal tissue serves as a water reservoir. The fact that the difference is less in the older zones and greater in the younger would seem to indicate that the flow of water from the epidermal tissue to the cortical tissue occurs more readily in the younger zones. It would thus appear that the young developing cortical cells, not far removed from the region of proliferation, can be quickly supplied with water from the older cortical cells and also from the epidermal cells of the same age.

The high average difference between the two tissues must not be interpreted to mean that the possible flow of water from the epidermis to the cortical tissue is necessarily great, because the nature of the walls of the two tissues is not the same, and it is quite possible that a sufficient resistance is offered by the walls to reduce the water current which is induced by the high potential difference of 5 atmospheres. If it were possible to determine the resistance of the wall to the flow of water and incorporate it in the gen-

[5] Experimental evidence of the correctness of the interpretation, that is of the flow of sap as indicated by the gradient, was obtained by administering sugar solutions of slightly greater osmotic pressure than the recorded suction tension of the cells in the uppermost zones, and it was noted that the hypocotyls wilted; the wilting being noted first directly above the soil, and then it progressed steadily to the uppermost zone. These facts indicate that the flow of water was reversed, passing from the upper zones to the next lower zones.

eral equation (2) as a part of the term A, the final potential difference between the two tissues would undoubtedly be less than 5 atmospheres.

The average potential difference between the epidermal cells from zone to zone is only 0.3 atmosphere, whereas the difference from epidermal tissue to cortical tissue is approximately 5 atmospheres. This is rather surprising, since the potential difference vertically must be sufficient to cause the water to ascend against the force of gravity and also to overcome the resistance of the horizontal cell walls. It is difficult to see how the water could rise in the epidermal cells unless a wall resistance to the flow of water from the epidermis to the cortical tissue is assumed. This assumption would presuppose that the nature of the vertical walls of the epidermal tissue is different from the horizontal walls of the epidermal cells. This assumption is not too bold in view of the fact that it is well known that cell walls do not grow much horizontally, but do grow vertically (17). We might then well assume that the vertical walls offer a great resistance to the flow of water, but the horizontal walls offer less resistance, so that the water flows more readily vertically into a given epidermal cell than it does from the same cell horizontally, in spite of the greater horizontal potential difference. It may further be assumed that the wall resistance to water flow from epidermal tissue to cortical tissue increases with the development of the cell wall, i.e. it is greatest in mature cells and least in young cells. In the older cells where, as was previously shown the difference between the Si_n values for the two tissues is least and the wall resistance to water flow is probably greatest, there is not so great a tendency of water to flow from the epidermis to the cortical tissue in spite of the potential difference indicated by Sz_n differences (see table 4, col. 6, 7) as there is in the younger cells.

THE WALL PRESSURE AND THE NATURE OF THE WALL

The wall pressure is a vector which acts antagonistically to the hydrostatic pressure and tends to diminish or to prevent entirely the influx of water into the cell sap cavity. When the cell is in the state of incipient plasmolysis its scalar value is evidently zero, but in the saturated state it is maximum, and it is equal to the hydrostatic pressure or to the osmotic pressure of the cell sap (Si_s). Assuming that the increment of the wall pressure, from incipient plasmolysis to the saturated state, is proportional to the change in the volume of the cell, the wall pressure of the normal cell can be determined according to the equation:

$$W_n = W_s \times \frac{V_n - V_g}{V_s - V_g} \tag{3}$$

in which W_n is the wall pressure in the normal state; W_s, the wall pressure in the saturated state; $(V_n - V_g)$, the change in volume from the normal state to the state of incipient plasmolysis; and $(V_s - V_g)$, the change in volume from the state of plasmolysis to the state of saturation.

From the formula it is evident that the contraction and the expansion of the cell wall are important factors which influence the value W_n. If the cell wall is extensible it offers little resistance, so that $V_s - V_g$ is relatively great and the value of W_n is proportionately small; furthermore, under this condition the influx of water is relatively great and the osmotic pressure (which is numerically equal to W_s) of the cell sap at saturation is correspondingly low, so that both factors tend to make W_n relatively low when the walls are plastic and extensible. If the walls are not plastic, but elastic, $V_s - V_g$ becomes less, W_s becomes greater and W_n becomes greater in consequence. The rate of increment will depend upon the coefficient of elasticity of the cell wall. When the walls are rigid, or only slightly elastic $V_s - V_g$ is small, and W_s not much different from Si_g, i.e. relatively high. In consequence W_n is great and the rate of increment from zero to maximum is great.

From these considerations it is evident that the values obtained for W_n should indicate, to some extent at least, the nature of the cell walls in the various stages of cell development; but W_s depends also upon the capacity of the cell and on the solute produced during the cell's growth, it may not be assumed that the variations of W_n give an exact expression of the variations of the modulus of elasticity of the wall.

In this connection it should be recalled that the discovery by Ursprung and Blum (47) that turgor was minimum in the zones of vigorous growth created surprise only because the nature of the osmotic quantities and the nature of growth by cell enlargement were so little understood at the time. Now that the osmotic relations are better understood and our knowledge of the structure of the cell wall in the various stages of the cell's development has advanced their results appear to be as they should be, and the old and widely held view that cell enlargement is entirely due to the hydrostatic pressure from within is untenable.

These facts must be borne in mind during the interpretation of our results. While it cannot be claimed that the wall pressure gives quantitative expression of the plasticity, the rigidity, or the coefficient of elasticity, nevertheless the results give some evidence of the condition of the wall in the various stages of the development of the cell, and are not contradictory to the known facts regarding it.

Ursprung and Blum's discovery of minimum turgor in the zone of maximum growth gave the first experimental evidence that the wall must grow actively during the process of growth by cell enlargement. The reader is referred to the reviews of the literature on this subject by Frey-Wyssling (21) and by Anderson (1). Undoubtedly the biochemical regulator auxin induces the active growth of the cell wall, but with time it is becoming more evident that the material added to the wall is elaborated by the protoplast. Not only is the mass of the wall changed during growth but its nature also;

the extensibility, the elasticity, and the rigidity are all modified. Heyn (28) and Söding (39) produced conclusive evidence that the changes in the nature of the cell wall are not, however, primary causes of growth. Gessner (23) also showed that a change in extensibility must be considered a phenomenon of growth and not its cause. The data which we present are not intended to prove these facts, but they are in agreement with them and serve well to illustrate them.

In table 5, the results obtained for W_n are given for the two tissues. Considerable experimental error was discovered in our data for the cortical tissue in the sixth zone and conditions prevented a repetition of the experiment so that the space for that value was left blank.

In the examination of our data it must not be forgotten that although the hydrostatic pressure is not the cause of growth, it is, like the increment in the wall and the changes in the wall's nature, a growth phenomenon. Unless solute were produced as cell enlargement proceeds the turgor could not well be maintained. As previously stated Beck, Lonsing, and Andrus (10, 14) proved that the production of solute is proportional to the growth. The importance of the solute as a factor in the production of wall pressure is evident from the equation:

$$W_n = Si_n - Sz_n \qquad (1)$$

in which W_n is the wall pressure; Si_n, the suction tension of the contents of the cell; and Sz_n the suction tension of the cell as an entity. From a comparison of the Si_n values given in table 3, the Sz_n values given in table 4, and the W_n values given in table 5, it becomes evident that the relatively low Sz_n values for both tissues in the growing zones are undoubtedly determined by the changes in the nature of the wall rather than by changes in the rate of solute production. To make this more evident these different values have been plotted against the distance from the cotyledons (see figure 5). If the cell were not to change its volume and if the nature of the wall were to remain the same, the maximum (Sz_n) and the minimum turgor in the region of greatest growth could not be explained because the turgor should in that case increase proportionately with the solute production. This, however, not being the case, the changes in the wall must be assumed actually to occur. The changes might be in the volume of the cell, or in the nature of the cell wall, or in both.

In table 5, the normal wall pressure and the pressure of the saturated cell are recorded. The normal wall pressure is given as derived from equation (1) in which Sz_n was obtained by direct experiment and Si_n as previously explained. It is also given as obtained by calculation according to equation (2). For both tissues the results obtained by the two methods are of the same order and of nearly the same value.

The W_s is recorded only for the purpose of giving the quantities necessary for checking the results. As previously explained they represent the

osmotic pressure of the cell sap at the point of saturation. Since the forces involved are not purely osmotic in the first zone and to some extent in the second, the actual W_s is probably lower than the recorded value. Since W_s is an implicit function in equation (3) the value of the explicit function W_n must be too high for these two zones. The results obtained by equation (1) (in which W_s is not involved) can be considered as being obtained by direct experiment. They are actually somewhat lower than those obtained by equation (2). They are, nevertheless, too great, because the values Si_n and Sz_n also involve non-osmotic forces in these two zones. We have no means of determining exactly how much lower the two values actually are. The fact

TABLE 5. *The Wall Pressure of the Developing Epidermal and Cortical Cells in the Hypocotyl of Helianthus Seedlings in the Normal State (W_n) and in the Saturated State (W_s).*

Zone	(W_n) Epidermis: Derived from Equation $Si_n - Sz_n = W_n$	(W_n) Epidermis: Calculated from Equation $W_n = W_s \times \frac{V_n - V_g}{V_s - V_g}$	(W_n) Cortical: Derived from Equation $Si_n - Sz_n = W_n$	(W_n) Cortical: Calculated from Equation $W_n = W_s \times \frac{V_n - V_g}{V_s - V_g}$	(W_s) Epidermis: Experimental	(W_s) Cortical: Experimental
1	2.0	2.13	0.235	0.257	7.24	10.06
2	1.44	1.4	0.210	0.344	6.29	10.00
3	1.39	1.22	0.120	0.137	6.43	9.46
4	1.14	1.12	0.120	0.255	6.08	8.47
5	2.05	2.03	0.42	0.355	5.93	8.56
6	2.28	2.18			6.02	8.26
7	2.58	2.4	0.42	0.390	6.05	7.72

that we failed to obtain minimum turgor at the point of maximum rate of enlargement, i.e. 6.5 mm. from the base of the cotyledons or in the uppermost region of the second zone (10, 14), is, no doubt, due to the involvement of non-osmotic forces. Our actual minimum occurred in the fourth zone. This is particularly interesting because previously Beck and Donnelly (13) established the fact that in strictly comparable plants a critical point occurs beyond which the cells respond with great difficulty to geotropic stimulation. The point is well defined and is located 25 mm. from the base of the cotyledons, or at the end of the fifth zone. Our results and those of Beck and Donnelly clearly indicate that some critical change must occur in the nature of the cell walls which is initiated in the fourth zone and is almost completed in the fifth. If it be assumed (and the assumption is in harmony with our results) that beyond the fourth zone the cells become rigid, the reason for the sharp point of demarcation is given. In the lowermost four zones the

steady increment of the wall pressure is very evident; this is, no doubt, due to the increasing rigidity of the wall. This becomes more evident when it is borne in mind that it is precisely in this region that the ability of the cells to expand when gorged with water (see figure 2) and the change in concentration of the sap from O_n to O_g or $O_n - O_g$ becomes less (see table 2). From these results and considerations it follows that if Ursprung's statement, that the turgor is minimum when the growth rate is maximum, must be taken as strictly correct, it cannot be arrived at by purely plasmolytic methods such as we employed. According to our data the minimum turgor does not occur in a sharply defined manner, so that low turgor extends through the second, third, and fourth zones. The actual minimum is in the fourth zone for the epidermis and in the third for the cortical tissue.

The Modulus. The variations in the wall pressure indicated changes in the physical nature of the cell wall. It is desirable to express such changes in the variation of a modulus. This is, however, always difficult, if at all possible. The volume modulus expresses the restoring force which is evoked by a given change in the mean distance between the molecules, the configuration remaining unchanged. The rigidity modulus measures the restoring force produced by a change in the relative position of the molecules without changing the mean distance. Ordinarily a cross between the two is employed for practical purposes, which is known as Young's modulus. None of these can easily be applied for the interpretation of our data. The data do, however, permit us to express the strain produced by a given stress, and this is what the modulus essentially expresses. It is necessary in the expression of a modulus that the material be not strained beyond the limits of elasticity. Now, our data gave unequivocal evidence that in the first and second zones the turgor stretches the walls beyond the limits of elasticity, so that the figures for these zones might well be questioned. Since it is difficult to verify if the walls have been stretched beyond the limits of elasticity, it is more reliable to employ the figures obtained for the relative contraction rather than those for relative expansion.

In figure 2 the relative expansion and contraction obtained in the various zones for the two tissues is given in graph form. The original sizes were determined while the specimen was immersed in paraffin oil. The expansion was obtained by permitting the cells to gorge themselves with water. The contraction was obtained by placing the specimen in the plasmolyte of the exact O_g concentration.

A study of figure 2 makes it evident that the cortical tissue expands more readily than does the epidermis. In the first four zones it also contracts more readily than the epidermis, but not so in the older zones. In harmony with the conclusion arrived at from the study of the wall pressures these graphs also indicate very evident changes which take place in the nature of the cell

walls, particularly in the third and fourth zones. It was precisely in these zones also where great difficulty was experienced in the exact determinations of the osmotic values by the method of averages and great care had to be exercised. It is now evident that the cells of the fourth zone are in a critical state and difficulty in obtaining consistent results will be experienced if one is not extremely careful to work the determinations exactly at the location within the limits indicated.

Since the cortical tissue expands readily in the first three zones and also contracts to a fair extent (in fact more than in older zones) but not nearly in the same degree as the expansion, it follows that this tissue is plastic but possesses a slight degree of elasticity, and is practically non-rigid, in the first three zones. The epidermal tissue, however, loses in extensibility, but does not lose much in contractibility which would indicate that in the first and second zones this tissue is plastic and is practically non-elastic. The plasticity of the first and second zones can also be detected by attempting to break the hypocotyl in these regions. It breaks very easily under a bending or stretching stress in these zones. Both tissues are therefore practically devoid of elasticity and rigidity in the younger zones. Beyond the fourth zone the hypocotyl is more tenacious and does not break readily under a bending stress or stretching stress.

In table 6 moduli for the various zones are deduced by the equation:

$$M = \frac{W_n}{\frac{L_n - L_g}{L_g}} \tag{4}$$

in which M is the modulus; W_n, the normal wall pressure (stress); and $\left(\frac{L_n - L_g}{L_n}\right)$, the change in length per unit length (strain) from the length at incipient plasmolysis to the normal length.

TABLE 6. *Moduli of the Cell Walls of the Hypocotyl of Helianthus Seedlings.*

ZONES		1	2	3	4	5	6	7
MODULUS EQUATION: $M = \frac{W_n}{\frac{L_n - L_g}{L_g}}$	Epidermis	112.11	134.6	50.6	62.2	81.2	121.1	160.0
	Cortex	16.06	13.23	4.02	13.42	55.5		65.0

In figure 4 the moduli for the two tissues are plotted against the distance from the base of the cotyledons. From this figure it at once becomes evident

that the epidermis in general is more rigid than the cortical tissue and that both tissues begin to become more rigid in the third zone and increase steadily in rigidity up to the maximum in the mature cells. The results are in harmony with the notions that the epidermis is mainly a protective tissue and can serve as a reservoir of water and that the cortical tissue is a dynamic one and readily takes up and gives off water particularly in the younger zones.

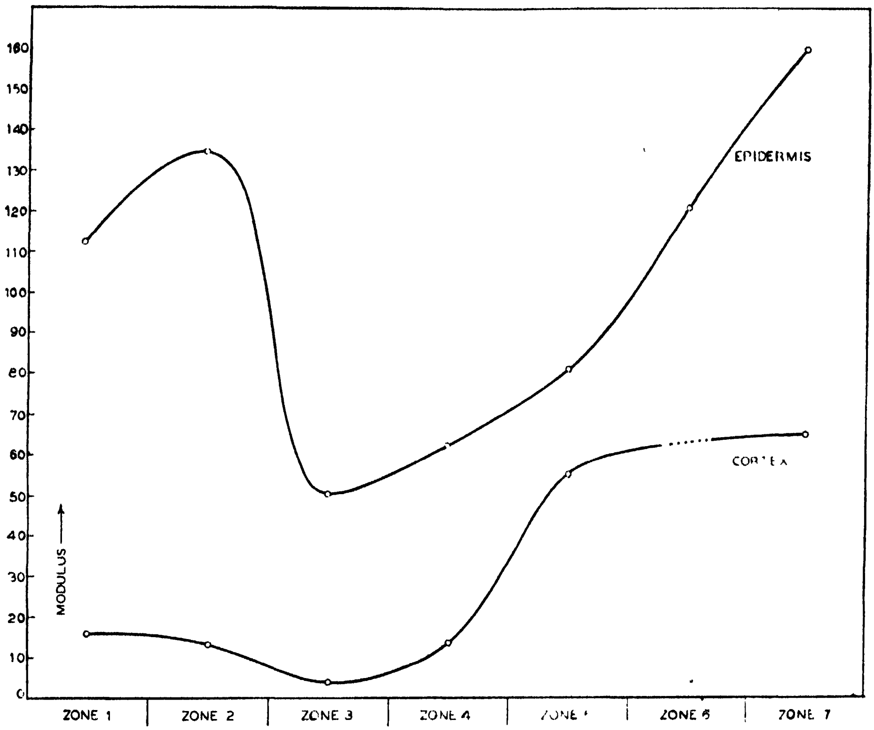


FIG. 4. Moduli of the cell walls of the hypocotyl of *Helianthus* seedlings plotted against the age of the cells.

SUMMARY AND CONCLUSIONS

A diagram of the seedlings was made to give the dimensions and show the zones in which the osmotic quantities of the epidermis and cortex were determined. The youngest cells, that is, those of the first and second zones, contained carotinoid pigment but no chlorophyll. These pigments may form a part of the respiratory mechanism and influence the production of auxin.

The determinations of the sizes of the cells proved that they grow by enlargement in the characteristic manner, the maximum rate being at the point 6.5 mm. from the base of the cotyledons, i.e. in the uppermost region of the second zone. The region of cell proliferation does not extend much

beyond 1 mm. from the base of the cotyledons, i.e. the uppermost region of the first zone. The active growth of the walls by intussusception is a fact. Turgor is not the source, or at least not the sole source of energy which causes cell enlargement. The active growth of the wall explains why the minimum turgor exists in the region of maximum growth. The transverse cell walls do not increase their mass appreciably but the lateral walls do. The active growth of the lateral walls, their plastic condition, the high suction tension, and low turgor in the young cells, explain the fact that the hypocotyl is less in diameter in the first zone (see figure 1). Solute is produced in proportion to cell enlargement. The cell sap cavity is small and the forces resembling osmotic forces are really non-osmotic in nature.

The following parallel gradients were established:

1) The plasmatic gradient; maximum viscosity being in the youngest cells.
2) Swelling gradient; greatest swelling power being in the protoplasm of young cells.
3) Electrical potential gradient; the greatest potential being in young cells.
4) Suction tension gradient; maximum suction tension being in the actively growing regions.

There are radial gradients: the concentration of the sap increases from the epidermis to the cortex; the O_g and Sz_n gradients are similar to the Si_n gradient.

The walls of the very young cells are plastic and extensible, while the older ones are less plastic and more elastic, and the mature ones are slightly elastic and almost rigid or non-extensible. All of these effects are probably the result of the activity of the protoplasm which is influenced by the auxin. The auxin need not necessarily be conducted to the protoplasm but may exercise its effects inductively in a physico-chemical manner comparable to the manner in which "evocators" are supposed to operate in animal tissues. It is probable that the chromatin of the young proliferating cells is involved in the process of growth by cell enlargement. The walls of the cortical cells are more extensible than those of the epidermal cells. They are able to contract more than those of the epidermal cells while young, that is, in the uppermost three zones. The walls of the cortical cells are always less rigid than those of the epidermal cells (see figure 4). A critical change begins to manifest itself in the nature of the walls in the third zone, but it does not create an appreciable change in the normal wall pressure until later, i.e. in the fourth zone (see figures 4, 5) where the rate of change is marked. This change explains the critical point at which quick response to geotropic stimulation ceases, namely 25 mm. from the base of the cotyledons. The concentration of the cell sap is maximum when the size of the cell is minimum, and vice versa. This may not be explained on the basis of increased capacity of the cell alone, because the production of solute is in proportion to the growth. O_g, O_n, and O_s are consistently higher in the cortex (see table 2) but the

difference becomes smaller with the age of the cell. In the mature zones the difference is slight (see figure 3).

The suction tension of the cell as an entity is maximum in the youngest zones and minimum in the mature, so that a gradient in the direction of the flow of water is established. A similar gradient exists from the epidermis to the tissues that lie within. The greatest potential difference between the tissues exists in the youngest cells and it is least in the mature cells. If the resistance which the walls offer to the current strength of the waterflow is disregarded, it appears that the water can flow upward in the epidermis and inward to the cortex. It is probable that the older cell walls offer considerably more resistance to the current than do the young cell walls, so that the inward flow is probably considerably less in the older cells than in the younger ones.

The maximum potential difference in suction tension between cells of the same tissue is between the fourth and fifth zones for the epidermis, and the third and fourth for the cortical tissue. This can be explained by the critical changes which take place in the walls of the cells in the respective regions.

The results recorded for the wall pressure give evidence of the changes in the physical nature of the wall during the process of cell enlargement. The results for the turgor are in general agreement with the claims of Ursprung and Blum that it is minimum in the region of active growth. The minimum is not exactly at the point where the rate of enlargement is maximum (6.5 mm. from the base of the cotyledons) but in the fourth zone where the critical changes in the physical nature of the wall occurs, and where the quick response to geotropic stimulation ceases. The turgor is maximum in the mature cells, where the walls are rigid.

In figure 5 the sizes of the cells (L_n) and the values of the osmotic quantities which are of chief interest, namely, the wall pressure (W_n), the suction tension of the normal cell sap (Si_n), and the suction tension of the cell (Sz_n) were plotted against the age of the cells, to give a summary view of their relationships during the process of enlargement.

A summary of the conditions of the cells and the osmotic quantities in the various zones (see figure 1) can be given as follows:

Zone 1. The diameter of the hypocotyl is minimum. The cells contain carotinoid pigment which might form a part of the respiratory mechanism. The uppermost region, approximately 1 mm. in length is the region of cell proliferation; the cells are compressed in appearance, show mitotic figures and lack a cell sap cavity. In the remaining part of the zone the cells fail to divide and begin to enlarge. The protoplasm of the cells is of maximum viscosity as is its swelling power, and its electrical charge. The cell wall is more intimately united with the protoplasm than in the succeeding zones, and plasmolysis is more difficult and takes a longer time. The walls are plastic

and extensible. The hypocotyl breaks easily under a bending or stretching stress. The forces which tend to supply water are largely non-osmotic in nature. The O_g, O_n, O_s, and Sz_n are maximum for both tissues. The respective differences in these quantities for the two tissues are in favor of the cortex and are maximum in this zone. Water flows readily from the epidermis to the cortex.

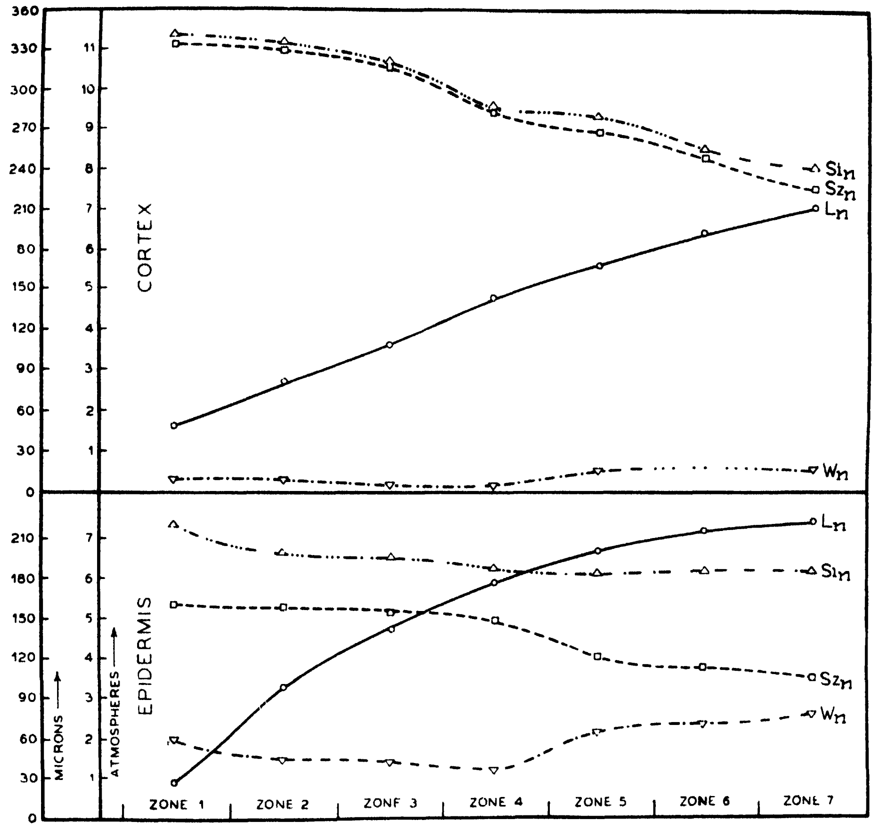


FIG. 5. Size of the cells (L_n), wall pressure (W_n), suction tension of the sap (Si_n), and suction tension of the cells (Sz_n), correlated with the age of the cells of *Helianthus* seedlings.

Zone 2. This zone contains the point of maximum rate of enlargement; it is located at 6.5 mm. from the cotyledons or 1.5 mm. from the upper limit of this zone. The cells contain a slight amount of carotinoid pigment. The viscosity of the protoplasm, the electrical charge, are less, in accord with the described gradients. The O_g, the O_n the O_s, and the Sz_n also decrease according to their respective gradients. The plasticity of the walls is still considerable, the elasticity and rigidity are negligible, the turgor is improved par-

ticularly in the lowermost part of the zone, where a bending or a stretching stress tends to break the hypocotyl less readily.

Zone 3. The protoplast and osmotic quantities change according to the described gradients. The rigidity of the cell walls is negligible, but there are indications of definite increment in rigidity which comes to clear expression in the fourth zone (see figure 4) where it manifests its influence on the wall pressure and the suction tension (see figure 5). The Sz_n potential difference is maximum for the epidermis in this zone.

Zone 4. Critical changes in the nature of the wall manifest their effects in this zone; they act disturbingly in the process of determining the osmotic quantities so that unusual care is necessary in the work. The critical point where the response to the geotropic stimulation fails to follow quickly is in this zone. The walls are no longer plastic, but are somewhat elastic. The Sz_n potential difference is maximum for the cortical tissue.

Zone 5. The elasticity of the walls decreases and the rigidity increases. The rate of increase is greater in the epidermis than it is in the cortical tissue (see figure 4).

Zone 6. The cells are almost mature. The cell walls are only slightly elastic and more rigid.

Zone 7. The cells are of maximum size, and the amount of solute present is also maximum. The wall pressure, turgor, and rigidity of the wall are maximum, but the concentration of the sap (O_n) and the suction tension of the cell (Sz_n) are minimum. The walls are hardly extensible, only slightly elastic, and the degree of rigidity is high, particularly in the epidermis (see figures 4, 5).

INSTITUTUM DIVI THOMAE
BRADLEY HALL
PALM BEACH, FLORIDA

Literature Cited

1. **Anderson, D. B.** The structure of the wall of higher plants. Bot. Rev. **1**: 52–76. 1935.
2. **Beck, Wm. A.** Cane sugar and potassium nitrate as plasmolyzing agents. *Protoplasma* **1**: 15–72. 1926.
3. ————. Osmotic pressure, osmotic value, and suction tension. Plant Physiol. **3**: 413–440. 1928.
4. ————. The effect of drought on the osmotic value of plant tissues. Protoplasma **8**: 70–126. 1929.
5. ————. Variations in the O_g of plant tissues. Plant Physiol. **6**: 315–323. 1931.
6. ————. Effect of light and atmosphere on the development of plant pigments. Stud. Inst. D. Thom. **1**: 217–244. 1937.
7. ————. Development of plant pigments in seedlings grown in the dark. Stud. Inst. D. Thom. **1**: 109–116. 1937.

8. ———————. Development of carotinoid pigment without the aid of light. Plant Physiol. **12:** 885–886. 1937.

9. ———————. Pigments formed in etiolated sunflower seedlings. Protoplasma **28:** 273–283. 1937.

10. ———————. Production of solutes in growing epidermal cells. Plant Physiol. **16:** 637–642. 1941.

11. ———————. Effect of drought on the production of plant pigments. Plant Physiol. **17:** 487–491. 1942.

12. **Beck, Wm. A. & Donnelly, W.** The *Helianthus* test. Stud. Inst. D. Thom. **2:** 179–189. 1939.

13. ———————. Bending and cell enlargement in the hypocotyl of *Helianthus annuus*. Stud. Inst. D. Thom. **2:** 259–281. 1939.

14. **Beck, Wm. A., Lonsing, A. & Andrus, B.** Solute production in growing cortical cells of *Helianthus annuus* seedlings. Stud. Inst. D. Thom. **3:** 113–129. 1941.

15. **Beck, Wm. A., Redman, R. & Schroeder, P.** Relation between the development of chlorophyll and time of exposure to light. Stud. Inst. D. Thom. **1:** 245–251. 1937.

16. **Bennet-Clark, T. A., Greenwood, A. D. & Barker, J. W.** Water relations and osmotic pressures of plant cells. New Phytol. **35:** 277–291. 1936.

17. **Borgström, Georg.** The transverse reaction of plants. 1939.

18. **Cholnoky, B. V.** Untersuchungen über den Plasmolyseort der Algenzellen: IV. Die Plasmolyse der Gattung *Oedogonium*. Protoplasma **12:** 510–523. 1931.

19. **Czaja, A. Th.** Polarität und Wuchsstoff. Ber. Deuts. Bot. Ges. **53:** 199-220. 1935.

20. **Derry, El. B.** Plasmolyseform und Plasmolysezeitstudien. Protoplasma **8:** 1–49. 1929.

21. **Frey-Wyssling, A.** Die Stoffausscheidung der höheren Pflanzen. Monograph. Ges. Physiol. Pflanzen Tiere **32:** 378. 1935.

22. ———————. Der Aufbau der pflanzlichen Zellwände. Protoplasma **25:** 261–300. 1936.

23. **Gessner, F.** Wachstum und Wanddehnbarkeit am *Helianthus* Hypokotyl. Jahrb. Wiss. Bot. **80:** 143–168. 1934.

24. **Gundel, W.** Chemische und physikalisch-chemische Vorgänge bei geisches Induktion. Jahrb. Wiss. Bot. **78:** 623–664. 1933.

25. **Gustafson, F. G.** Hydrogen-ion concentration gradient in plants. Am. Jour. Bot. **11:** 1–6. 1924.

26. **Hecht, K.** Studien über den Vorgang der Plasmolyse. Beitr. Biol. Pflanzen **11:** 137–192. 1912.

27. **Heilbrunn, L. V.** An outline of physiology. 1938.

28. **Heyn, A. N. J.** Der Mechanismus der Zellstreckung. Rec. Trav. Bot. Néerland. **28:** 113–244. 1931.

29. **Oppenheimer, H. R.** Kritische Betrachtungen zu den Saugkraftmessungen von Ursprung und Blum. Ber. Deuts. Bot. Ges. **48:** 130. 1930.

30. **Overbeck, F.** Studien über die Mechanik der geotropischen Krümmung und des Wachstums der Keimwurzeln von *Vicia Faba*. Zeits. Bot. **18:** 401–451. 1925.

31. **Pfeiffer, H.** Der gegenwärtige Stand der kolorimetrischen Azidimetrie in der Gewebephysiologie. Protoplasma **1:** 434–465. 1926.

32. ———————. Einzellreihige Pflanzenhaare zur Demonstration hysteretischer Effekte. Protoplasma **15:** 24–28. 1932.

33. ———————. Kleine Beiträge zur Bestimmung des I. E. P. von Protoplasten: VI. Das aufsuchen von Fällungen nach Einwirkung acidimetrisch abgestufter Puffer und Salzlösungen. Protoplasma **16:** 237–243. 1932.

34. **Reinhardt, M. O.** Plasmolytische Studien zur Kenntnis des Wachstums der Zellmembranen. Festschrift für Schwendener. 1899.
35. **Ruge, U.** Untersuchungen über den Einfluss des Heteroauxins auf das Streckungswachstum des Hypokotyls von *Helianthus annuus*. Zeits. Bot. **31**: 1. 1937.
36. ———. Untersuchungen über die Änderungen der osmotischen Zustandsgrössen und der Membraneigenschaften des Hypokotyls von *Helianthus annuus* beim normalen Streckungswachstum. Planta **27**: 352–366. 1937–1938.
37. **Ruhland, W. & Wetzel, K.** Zur Physiologie der organischen Säuren in grünen Pflanzen: III. *Rheum hybridum* Hort. Planta **3**: 765–769. 1927.
38. **Small, J.** Hydrogen-ion concentration in plant cells and tissues. Protopl.-Monogr. **2**: 1929.
39. **Söding, H.** Wachstum und Wanddehnbarkeit bei der Haferkoleoptile. Jahrb. Wiss. Bot. **74**: 127–151. 1931.
40. **Stark, O. K.** What is osmosis? Science **67**: 556–557. 1928.
41. **Strugger, S.** Über Plasmolyse mit Kaliumrhodanid. Ber. Deuts. Bot. Ges. **50**: 24–31. 1932.
42. ———. Beiträge zur Physiologie des Wachstums: I. Zur protoplasma-physiologischen Kausalanalyse des Streckungswachstums. Jahrb. Wiss. Bot. **79**: 406–471. 1933–1934.
43. **Ursprung, Alfred.** The osmotic quantities of the plant cell. Proc. Int. Cong., Ithaca **2**: 1081–1094. 1929.
44. ———. Handwörterbuch der Naturwissenschaften. ed. 2, 493–510. 1932.
45. ———. Die Messung der osmotischen Zustandsgrössen pflanzlicher Zellen und Gewebe. Handbuch der Biologischen Arbeitsmethoden, 1109–1572. 1937.
46. **Ursprung, Alfred & Blum, G.** Über die Verteilung des osmotischen Wertes in der Pflanze. Ber. Deuts. Bot. Ges. **34**: 88–104. 1916.
47. ———. Eine Methode zur Messung des Wand- und Turgordruckes der Zelle, nebst Anwendungen. Jahrb. Wiss. Bot. **63**: 1–110. 1924.
48. **Weber, Fr.** Das Fadenziehen und die Viscosität des Protoplasmas. Österr. Bot. Zeits. **70**: 172–180. 1921.
49. ———. Protoplasmatische Pflanzenanatomie. Protoplasma **8**: 291–306. 1929.
50. ———. Plasmolyse-Ort. Protoplasma **7**: 583–601. 1929.
51. ———. Plasmolyse und "Surface precipitation reaction." Protoplasma **15**: 522–531. 1931.
52. ———. Plasmolyse Permeabilität bei Kälte. Protoplasma **16**: 517–521. 1932.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 6, pp. 599–604 NOVEMBER, 1943

A NEW CONSTITUENT IN WHEAT GERM OIL

H. H. BUNZELL

In the course of our study of the vitamins present in wheat germ oil we found that wheat germ oil has a stimulating effect on the action of potato tyrosinase. This is true whether we use wheat germ oil extracted in the laboratory with ether and petroleum ether, or commercial wheat germ oil pressed (Abbott's Medicinal Wheat Germ Oil), or wheat germ oil extracted by ethylene dichloride (VioBin Corporation).

This phenomenon seems significant because of the various physiological functions with which, according to recent work, the copper enzyme, tyrosinase, seems to be concerned. Perhaps the most outstanding of these relationships is the destructive effect of tyrosinase on the vaso constrictor substance —hypertensin (8) and the oxidation of estrogens and their complete inactivation (9).

TECHNIQUE

The methods used were based on work described in earlier articles (2, 3). The simplified catox apparatus used in these experiments is shown in figure 1,[1] and has been described before (4, 7). The constant temperature chamber has also been described elsewhere (7).

The potato juice was pressed out by hand from ground peelings and was diluted with four volumes of water. In this dilution the tyrosinase activity was 0.101–0.166 Bunzell units (2, p. 40). The oxidase reagent used in this experiment was pure p-cresol. The reason for the choice of p-cresol in this connection was two-fold: one is that the mechanism of the oxidation of p-cresol by tyrosinase has been exhaustively studied by Nelson and collaborators (1). The other reason is that our work on the oxidases of potato tubers showed that p-cresol oxidation is influenced more than that of any other seventeen reagents used (5, 6).

All experiments were carried out in the presence of a phosphate buffer, pH 7. In control experiments a highly refined Russian mineral oil was used in place of wheat germ oil. In the effective experiment, dilution of the wheat germ oil when required was made with the same mineral oil.

PROCEDURE

Of the three compartments of the catox apparatus, the middle one was not used in these experiments. It served a useful purpose in assuring separation before deliberate mixing of materials placed in compartments 1 and 3. The following typical experiments will show the disposition of the materials:

[1] The plate for figure 1 was furnished by the author.

Experiment 1

In compartment No. 1: 1 cc. 20% potato juice.
In compartment No. 3: 0.022 g. p-cresol, 0.5 cc. buffer sol., 0.5 cc. Rus. min. oil.

Experiment 2

In compartment No. 1: 1 cc. 20% potato juice.
In compartment No. 3: 0.022 g. p-cresol, 0.5 cc. buffer sol., 0.0387 g. tocopherol in 0.5 cc. Rus. min. oil.

The constant temperature chamber was maintained at 35° C. The air vents (No. 7 in fig. 1) remained open until the temperature became adjusted, which required a little over a half an hour. The vents were then closed by turning the manometer (No. 5 in fig. 1) through 90° by inserting the hand through the trapdoor on top of the constant temperature box and beginning shaking, thereby mixing the components and initiating the reaction.

Rate of shaking was 140 excursions per minute; extent of excursion was 5.5 cm.

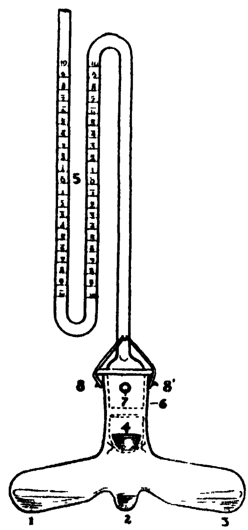


FIGURE 1

EXPERIMENTAL WORK

Readings were made as a rule at intervals of ten minutes and the experiments were of twenty-five to thirty minutes duration. For purposes of illustration a typical set of experiments is given in table 1. The data correspond to the conditions outlined under experiments 1 and 2 above.

Comparison of the final result obtained in experiment 2 with that obtained in experiment 1 shows an increase of 48%, due to the tocopherol preparation used. Throughout this paper only the last reading obtained at the end of twenty-five or thirty minutes will be used for comparison.

The selection of the proper quantity of p-cresol is important, because of its destructive effect on the tyrosinase when used above certain concentra-

TABLE 1. *The effect of tocopherol on potato tyrosinase*

Time in min.	Readings	
	Exp. 1 Control	Exp. 2 Tocopherol added
0	0.0	0.0
10	4.9	8.2
20	10.0	14.8
25	12.3	18.2

tions. For example, it was found that 0.0185 g. p-cresol used in an experiment gave a final reading of 14.0, while twice that amount, 0.0370 g., resulted in complete inhibition, presumably due to the destruction of the tyrosinase. We found it most satisfactory to use 0.022 g. p-cresol in each experiment, this being an innocuous amount and also easily measured in our calibrated micropipette.

Many experiments were performed, varying concentrations of the components of the system and also changing the physical conditions. Table 2 summarizes typical data. They are representative of all results obtained.

TABLE 2. *The effect of wheat germ oil on potato tyrosinase*

Addition	Final reading		Increase due to addition
	Control	"Addition"	
0.5 cc. wheat germ oil (made in this laboratory by extraction with ether and petroleum ether)	13.2	18.0	36.4%
0.5 cc. ditto	8.4	12.2	45.2%
0.5 cc. ditto	5.6	9.5	69.8%
0.5 cc. wheat germ oil (Abbott) pressed	13.6	18.55	36.4%
0.25 cc. ditto	12.05	16.1	33.6%
0.05 cc. ditto	13.4	17.5	30.6%
0.005 cc. ditto	11.45	13.85	21.0%
0.0005 cc. ditto	13.7	13.85	Insignificant
0.5 cc. wheat germ oil (VioBin Corporation) extracted	8.65	11.75	35.8%
0.05 cc. ditto	9.85	12.15	23.3%
0.005 cc. ditto	8.9	10.6	19.1%

All three kinds of wheat germ oil, even if used in only 1% solution (equivalent to 0.005 cc.), produced an increase in the rate of tyrosinase activity. Each set of results in table 2 represents a series of experiments carried out with fresh potato juice. There is considerable variation in the activity of the juice, since no attempt was made to use peelings of uniform thickness. This also explains why data showing an "increase" lack mathematical uniformity. Their significance is largely qualitative.

In all of the experiments here summarized, as well as all others tried, the increase in tyrosinase activity was accompanied by a difference in color. This was not observed where the difference between the control and "addition" experiments was insignificant (table 2, line 8). The reaction mixture of the control experiments was dark brown; that of the addition experiments, brick red. The dark red color could be extracted with methyl alcohol, indicating the presence of OH groups. Ether or chloroform extracts were colorless. The brick red color in the "addition" experiments was not soluble in alcohol, but gave a bright yellow solution with ether or chloroform. The bright yellow color of the extracts would indicate the presence of quinoid groups. There is every indication that in the stimulation experiments, there is not only a speeding up of the reaction, but also the formation of a different oxidation product.

Wheat germ oil contains, besides the vitamins of the E complex, vitamin A. To determine whether the vitamin A content of the wheat germ oil is related to the effect here described, we evaluated the vitamin A content of the VioBin wheat germ oil in terms of White's vitamin A preparation. The latter contained 108,100 U.S.P. units per gram. The comparison was made in a "Lumetron" electrical colorimeter using isopropyl alcohol as a solvent. It was found that a 10% solution of VioBin oil would contain per gram the equivalent of 0.00195 g. of the vitamin A oil used for comparison. This corresponds to a 0.2% solution of the comparison preparation. Table 3 shows results obtained at the end of thirty minutes. Experiments 1 and 3 are controls containing 0.022 g. p-cresol, 0.5 cc. water, 1 cc. 20% potato juice, and 0.5 cc. cotton seed oil. Experiments 2 and 4 contained the same reagents, except that the cotton seed oil was replaced by an equal amount of a 0.2% solution of vitamin A oil (White) in cotton seed oil. The amount of vitamin A in experiments 2 and 4 would equal that contained in the same volume of 10% VioBin wheat germ oil solution in cotton seed oil.

TABLE 3. *The effect of vitamin A on potato tyrosinase*

Experiment	1	2	3	4
Final reading	12.4	12.0	12.5	11.8

Comparing the average of 1 and 3, i.e., 12.45, with the average of 2 and 4, i.e., 11.9, we find that no increase is brought about by the vitamin A. This result is corroborated by the lack of any difference in coloration in the ultimate mixtures.

The next most obvious thought is that α tocopherol might be responsible for the effect. We secured a pure *d,l* α tocopherol from Merck and Company.

The material was weighed directly into the catox apparatus. Results are shown in table 4.

TABLE 4. *The effect of d,l α tocopherol on potato tyrosinase*

In each trial the following substances were used: 0.022 g. p-cresol, 0.5 cc. buffer, 1 cc. 20% potato juice, and Russian mineral oil and *d,l* α tocopherol as indicated below.

Experiment	1	2	3
	Control 0.5 cc. Rus. min. oil	0.0045 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil	0.0071 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil
Final reading	14.95	14.8	14.7
Experiment	4	5	6
	Control 0.5 cc. Rus. min. oil	0.0114 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil	0.0195 g. *d,l* α tocopherol in 0.5 cc. Rus. min. oil
Final reading	14.2	14.3	13.8

Results given in table 4 show that *d.l* α tocopherol (Merck) does not stimulate the action of tyrosinase. These results are corroborated by the fact that in both sets there was no difference in the color of the final reaction mixtures when the controls were compared with the corresponding tocopherol experiments. The color in all cases was dark brown.

We next tried a preparation of α, β, and γ tocopherol (Abbott Laboratories). This is made by the distillation of certain vegetable oils and contains 25% of a mixture of the three tocopherols. We have been unable to learn anything about the nature of the vegetable oils used besides wheat germ oil, nor have we been able to establish the relative amounts of α, β, and γ tocopherol in the mixture. Results are given in table 5.

TABLE 5. *The effect of α, β, γ tocopherol on potato tyrosinase*

In each trial the following substances were used: 0.022 g. p-cresol, 0.5 cc. buffer, 1 cc. 20% potato juice, and Russian mineral oil and α, β, γ tocopherol as indicated below.

Experiment	1	2	3
	Control 0.5 cc. Rus. min. oil	0.0335 g. α, β, γ tocopherol in 0.5 cc. Rus. min. oil	0.0387 g. α, β, γ tocopherol in 0.5 cc. Rus. min. oil
Final reading	12.3	16.7	18.2

The α, β, γ tocopherol preparation furnished by Abbott produced a pronounced increase in the tyrosinase activity. In experiment 2 (table 5) the increase was 25%, in experiment 3, 47.9%; the color in the control was the usual dark brown, while in the tocopherol experiments the color of the final reaction mixtures was brick red.

CONCLUSIONS

There is in wheat germ oil a constituent which speeds up the tyrosinase oxidation of p-cresol. This effect is not produced by the vitamin A in the oil or by the alpha tocopherol. It may be produced by beta or gamma tocopherol or by some other constituent of wheat germ oil. Owing to the extremely small concentration of vitamin K in wheat germ we are not inclined to attribute the effect to K. This point however, is being investigated in this laboratory.

Under the influence of the substance studied a different oxidation product is formed. This appears to be of quinoid character. It is possible that, in normal tyrosinase oxidation of p-cresol, the unstable hydroxyquinone formed as the third stage of the oxidation spontaneously disappears, while in the presence of the new component, it combines with it and thus becomes stabilized (10, pp. 198, 199).

BUNZELL LABORATORIES
NEW YORK

Literature Cited

1. **Bordner, C. A. & Nelson, J. M.** 1939. On the oxidation of p-cresol by means of tyrosinase. Jour. Am. Chem. Soc. **61**: 1507–1513.
2. **Bunzell, H. H.** 1912. The measurement of the oxidase content of plant juices. U. S. Dept. Agr., B. P. I. Bull. 238: 7–40.
3. ——————. 1912. The measurement of the oxidase content of plant juices. Jour. Am. Chem. Soc. **34**: 303–316.
4. ——————. 1914. A simplified and inexpensive oxidase apparatus. Jour. Biol. Chem. **17**: 409–411.
5. ——————. 1914. Oxidases in healthy and curly-dwarf potatoes. Jour. Agr. Res. **2**: 373–404.
6. ——————. 1916. The relative oxidase activity of different organs of the same plant. Jour. Biol. Chem. **24**: 103–110.
7. ——————. 1942. A simple method for B_1 determination. Ind. and Eng. Chem. (Anal. Ed.) **14**: 279–280.
8. **Croxatto, H. & Croxatto, R.** 1941. Inhibitory action of amine oxidase on the vasoconstrictor effect of hypertensin. Proc. Soc. Exptl. Biol. Med. **48**: 392–395.
9. **Graubard, M. & Pincus, G.** 1942. Steroid metabolism: Esterogens and phenolases. Endocrinology **30**: 265–269.
10. **Sumner, J. B. & Somers, G. F.** 1943. Chemistry and methods of enzymes. Academic Press, New York. pp. i–xi, 1–365.

BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 70, No. 6, pp. 605–611 NOVEMBER, 1943

CROSSING-OVER AND SECOND DIVISION SEGREGATION IN FUNGI

FRANCIS J. RYAN

In some fungi the segregation of genetic factors can be determined by the linear order in which different phenotypes are distributed among the "sexual" spores. When two mutant characters are found in the order A A a a the best interpretation is that the alleles responsible for them have separated in the first meiotic division. On the other hand when the arrangement is A a A a or A a a A they have separated in the second division (Dodge 1927; Wilcox 1928). Such second division segregations have been explained by many mycologists in terms of a disjunction of homologous chromosomes during the second meiotic division. Dodge (1940) has shown, however, that in many cases there is an equally possible alternative explanation which involves the more modern but now classical notions of first division disjunction and crossing-over. Despite Dodge's suggestion, there are two studies on inheritance in ascomycetes which apparently confirm with genetic data the old mycological point of view. Both Wülker (1935) and Zickler (1934), who are aware of the view now prevalent among geneticists that alleles may be reduced (separated) in either the first or second meiotic division, contend that second division disjunction of homologous spindle fiber attachments or kinetochores (centromeres) must also be invoked to explain their experiments with *Neurospora* and *Bombardia* respectively. This of course implies that each kinetochore is divided in the first division, an unprecedented happening in the normal meiosis of other organisms. To date no adequate refutation based upon an analysis of their extensive data has been made.

Zickler was fortunate in being able to determine certain genotypes among his ascospores without dissection and germination because some of the genes with which he dealt affected the color of the ascospores themselves as well as the mycelia they produced In a cross of the *viridis* and *lactea* mutants the arrangement of greenish and colorless spores in the intact ascus showed that second division segregation took place in 66.4 per cent of 2355 asci. This, Zickler pointed out, would occur if the separation of the four chromatids into pairs in the first meiotic division occurred at random. That is, each chromatid has an equal chance to associate with each of three others. Since only one of the others is a sister chromatid while two are non-sisters, first division segregation (association of sister chromatids) occurs half as frequently as second division segregation (association of non-sister chromatids).[1]

[1] Wülker believes the ratio would be 1 : 1 instead of 2 : 1 if the separation into pairs were random. His error lies in the fact that he considered only separations along the equa-

If Zickler's interpretation is correct then *all* factors, irrespective of their location on the chromosome, should show second division segregation in two thirds of the cases.

In a cross of *viridis* and *rubiginosa* mutants, however, 8204 asci containing greenish and reddish spores showed 64 per cent second division segregation. Zickler himself calculated that this percentage was significantly different from 66.7 per cent by statistical test. In an attempt to explain this discrepancy he concluded that something (external) must have influenced the random separation of the individual chromosomes or suppressed their longitudinal split.

Zickler may be correct in assuming that some uncontrolled (although perhaps genetic) variable is influencing the number of second division segregations. For *viridis, rubiginosa* and *lactea* are multiple alleles and, although he does not believe so, they would be expected to show the same percentage second division segregation. Nevertheless, the task at hand is to determine whether a second division disjunction is the necessary interpretation of these data.

The problem can be approached by an analysis similar to that which Lindegren (1933) used in his studies on *Neurospora*. Since color is linked with sex in *Bombardia* the percentage of new combinations of the two factors can be calculated and compared with the sum of one half of the percentages of second division segregation of these factors. (The percentages are halved in order to obtain values comparable to those secured in *Drosophila* where only one half of all cases of crossing-over are observed since only one of the four chromatids is recovered.) In the case of a first division disjunction with a single crossing-over these values are equal. For example, if we assume crossing-over to occur in all asci as outlined in figure 1, the genotypes recovered in the haploid spores would be AB, aB, Ab, and ab. Thus, there are 50 per cent new combinations. Second division segregation of A from a (A a A a) would occur in 100 per cent of the cases and this divided in half is 50. Here segregation of B from b in the second division (B b B b) never occurs and so the final value based on second division segregation is 50. This is exactly the same as that calculated on the basis of new combinations. When we assume crossing-over to occur only in some cases the values are smaller but still remain equal—each crossing-over results in a second division segregation so that two of four chromatids have new combinations of genes. From an agreement of this sort in *Neurospora*, Lindegren correctly concluded not only that there was crossing-over in the four strand stage but that homologous kinetochores separated in the first division.

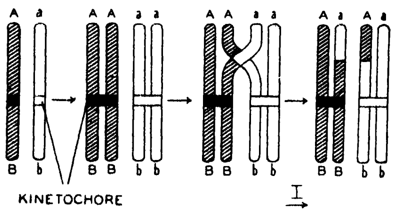
---

tional or reductional splits and failed to consider diagonal aggregations across both of these planes.

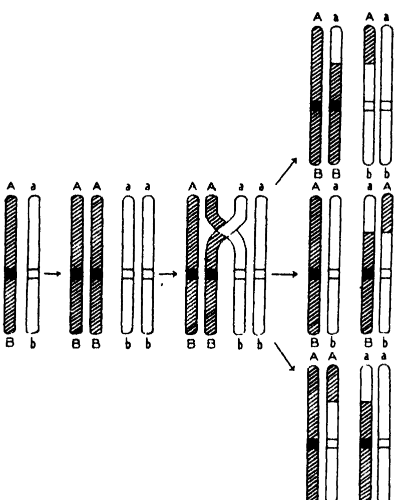
On the other hand, if it were granted that there is a random assortment of the four chromatids during meiosis as well as crossing-over, an hypothesis which Ziekler considered, then the above comparison yields very different results (fig. 2). Here the genotypes recovered and their order would be:

AB	aB	Ab	ab =	33.3%
AB	ab	aB	Ab =	33.3%
AB	Ab	aB	ab =	33.3%
				100.0%

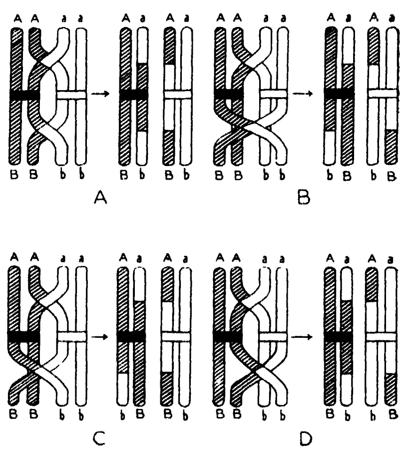
50 per cent of these are new combinations. However, since there is 66.7 per cent second division segregation of both A and B a value of 66.7 is obtained which is quite different from the value based on new combinations. If one



1



2



3

FIG. 1. Orthodox behavior of chromatids during the first meiotic division involving crossing-over and first division disjunction of homologous kinetochores (I). The kinetochores split in the second division. FIG. 2. Hypothetical behavior of chromatids during the first meiotic division assuming crossing-over and random segregation of kinetochores which split in the first division. FIG. 3. Double crossing-over with first division disjunction of homologous kinetochores which results in *old* and new combinations and second division segregation of genetic factors.

assumes that the attraction of *sister chromatids* is somewhat greater than that between non-sisters then there is a closer correspondence of values calculated by the two methods. The values eventually coincide when sister attraction is complete but this situation is identical with first division disjunction of kinetochores discussed in the paragraph above.

If we assume crossing-over to occur only in some cases the value of 66.7 is still obtained from second division segregations just as it was when we assumed either that there was no crossing-over or that crossing-over occurred in all of the cases. However, the value obtained from new combinations decreases in proportion to the decrease in percentage of crossing-over and in this way the discrepancy between the two values increases.

Thus a method seems available for determining whether a second division segregation is the result of a first or a second division disjunction of homologous kinetochores.

The only evidence which Zickler gives that could be put to this test is in a footnote. Here he states that there were only 37.1 per cent new combinations of color and sex in the *rubiginosa-viridis* cross. Zickler found 57.7 per cent[2] second division segregation of color and 62.7 per cent second division segregation of sex. These divided in half are arbitrary measures of the map distance of the loci from the kinetochores. Therefore 28.9 and 31.4 may be either added or subtracted according to whether the color and sex loci are on the same or opposite sides of the kinetochore. Since neither of the resultant values of 60.2 or 2.5 correspond with the map distance calculated from new combinations, Zickler concludes that crossing-over cannot explain the frequency of first and second division segregations.

Stripped to its essence, however, this lack of correspondence simply means either that all the second division segregations of *rubiginosa* from *viridis* did not result in new combinations with sex (60.2 compared with 37.1) or that all the new combinations were not the result of second division segregations (37.1 compared with 2.5). This is exactly what could be expected if double crossovers had occurred (fig. 3). Such crossovers can yield both new and *old* combinations and yet the result is always second division segregation. If we assume for the time being that the four possible types of double crossing-over occur in equal proportions then the following genotypes are obtained in the order shown:

---

[2] Zickler consistently found a smaller percentage of second division segregations of *viridis* from *rubiginosa* when he dissected and germinated ascospores than he found by direct count in the ascus. For example, in this experiment he found 57.7 per cent compared with 64.0 per cent—an even greater deviation from the 66.7 per cent predicted on the basis of random segregation of kinetochores. The discrepancy between results obtained by different types of analyses he likewise attributes to environmental influence.

AB	ab	AB	ab =	25%
Ab	aB	Ab	aB =	25%
Ab	aB	AB	ab =	25%
AB	ab	Ab	aB =	25%
				100%

There are 50 per cent new combinations. But there are 100 per cent second division segregations of both A and B so that a value of 100 is obtained to compare with 50. It is obvious there is a discrepancy resembling that between the values of 37.1 from recombinations and 60.2 from second division segregations obtained in the *viridis-rubiginosa* cross. (The value 2.5 will not be considered because it may not be significantly different from 0 and at any rate it is not predicted by the hypothesis of random segregation of homologous kinetochores.)

The discrepancy between the values for second division segregation and new combinations can be corrected by the use of the equation $m + n - 2\,mn = \%$ new combinations between color and sex (Haldane 1919) where m = map distance or recombination between color and kinetochore and n = map distance or recombination between sex and kinetochore. This is simply a subtraction of an estimate of the percentage of old combinations formed by double crossing-over which give rise to second division segregation (see figure 3) from the percentage of new combinations expected if there were no double crossing-over. Solving, $.289 + .314 - .181 = .422$, or 42.2 per cent new combinations are expected from the data on second division segregation when double crossing-over is taken into account and, as was assumed, crossing-over is random. This is rather close correspondence with the observed value of 37.1 per cent. The small difference between the two may be due to the presence of more double crossing-over than would be expected on the basis of chance. This would increase the value of mn in the equation and decrease the percentage of new combinations expected. Such an explanation seems reasonable in view of the fact that non-random crossing-over appears to occur among molds (Lindegren and Lindegren 1937, 1939; Whitehouse 1942)

It would be possible to determine decisively whether Ziekler's ratios were the result of double crossing-over, were it possible to analyze the genotypes and orders of spores from the *viridis* × *rubiginosa* cross. Unfortunately, Ziekler does not present his original data so that this point cannot be finally decided.

Wülker fortunately does present his original data on *Neurospora* and so it is possible to determine directly the proportion of ascus arrangements resulting from double crossing-over. Indeed, recognizing this possible interpretation, he carried out the analysis himself and showed how all the arrangements he found could be explained in terms of crossing-over. But

the presence of 28 asci resulting from three-strand crossing-over (fig. 3, C and D) compared with 8 asci resulting from two-strand crossing-over (fig. 3, A) and 8 resulting from four-strand crossing-over (fig. 3, B) seemed disproportionate to him. Consequently he made an elaborate estimate of the proper ratios of first and second division disjunctions combined with several types of crossing-over which would yield the ascus types he observed. It is not necessary to discuss these estimates because Wülker revealed the critical point for his hypotheses in these words which are freely translated—"The appreciation of all following calculations depends *alone* upon recognizing in the value of 28 asci a deviation from the numbers expected exclusively from crossing-over which cannot be explained in other ways." Accordingly, if it is possible to show that 28 asci resulting from three-strand crossing-over is not beyond expectation in Wülker's results, it is not necessary to accept his scheme for second division disjunction.

In the first place the total number of double crossovers across the kinetochore (it is impossible to calculate the expected percentage of crossing-over in one arm because only one gene was studied in each arm), 24.4 per cent, resembles that calculated from the frequency of single crossing-over, 24.8 per cent. Moreover, it can be seen from figure 3 that the expected ratio of two-, three- and four-strand double crossing-over occurring at random is 1 : 2 : 1. When a χ^2 test is applied to the fit of the 8 two-strand, the 28 three-strand, and the 8 four-strand double crossover asci to the 1 : 2 : 1 ratio a P of 0.2 is obtained indicating a good fit to the crossing-over hypothesis for such a small number of cases,[3] thus:

Number of strands involved in double crossing-over	2	3	4
Actual number of asci	8	28	8
Expectation (e)	11	22	11
Deviation (d)	3	6	3
d^2	9	36	9
$\frac{d^2}{e}$	0.82	1.64	0.82

$$\Sigma \frac{d^2}{e} = \chi^2 = 3.28 \qquad P = 0.2$$

We may conclude therefore that in *Neurospora* the genetic evidence indicates first division disjunction of kinetochores and crossing-over.

In summary, it is certain that Zickler's data on *Bombardia*, as presented, are not crucial in demonstrating either a first or a second division disjunction of homologous kinetochores. The crucial data for establishing first division disjunction—the recognition of double crossing-over—may be in his original records but are not presented in his report. Neither has he found the data crucial for a demonstration of a second division disjunction—

[3] It is interesting to note that Wülker's data on *Neurospora sitophila* provide no evidence for the non-random crossing-over found by Lindegren for *N. crassa*.

namely, that all factors irrespective of their location on the chromosome show second division segregation in two-thirds of the cases. In short, if single and double crossing-over occurs, as seems likely, the data can be explained on an orthodox genetic basis. Moreover, besides Wülker's demonstration that the ascus types he obtained in *Neurospora* can be explained in terms of first division disjunction and crossing-over, it is possible to show that even the ratios of these types to one another are as would be expected on this basis. This is critical evidence on behalf of first division disjunction of kinetochores.

Thus, there is every reason to believe that, in molds as in other organisms, homologous kinetochores separate in the first meiotic division (reductionally) and each kinetochore divides in the second division (equationally).

DEPARTMENT OF ZOOLOGY, COLUMBIA UNIVERSITY
NEW YORK

Literature Cited

Dodge, B. O. 1927. Nuclear phenomena associated with heterothallism and homothallism in the Ascomycete *Neurospora*. Jour. Agr. Res. **35**: 289–305.

Dodge, B. O. 1940. Second division segregation and crossing-over in the fungi. Bull. Torrey Club **67**: 467–476.

Haldane, J. B. S. 1919. The combination of linkage values and the calculation of distances between the loci of linked factors. Jour. Genetics **8**: 299–309.

Lindegren, C. C. 1933. The genetics of *Neurospora*. III. Pure bred stocks and crossing-over in *N. crassa*. Bull. Torrey Club **60**: 133–154.

Lindegren, C. C. & Lindegren, G. 1937. Non-random crossing-over in *Neurospora*. Jour. Hered. **28**: 105–113.

Lindegren, C. C. & Lindegren, G. 1939. Non-random crossing-over in the second chromosome of *Neurospora crassa*. Genetics **24**: 1–7.

Whitehouse, H. L. K. 1942. Crossing-over in *Neurospora*. New Phyt. **41**: 23–62.

Wilcox, M. S. 1928. The sexuality and the arrangement of the spores in the ascus of *Neurospora sitophila*. Mycologia **20**: 3–17.

Wülker, H. 1935. Untersuchungen über Tetradenaufspaltung bei *Neurospora sitophila* Shear et Dodge. Zeit. für Ind. Abst.-und Vererbungslehre **69**: 210–248.

Zickler, H. 1934. Genetische Untersuchungen an einem heterothallischen Askomyzeten (*Bombardia lunata* nov. spec.) Planta **22**: 573–613.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 612–614 NOVEMBER, 1943

THE NUMBER OF CHROMOSOMES IN TWO SPECIES OF AMORPHOPHALLUS

CLYDE CHANDLER

Plants of the genus *Amorphophallus* are native of the tropics. The giant forms of this genus are quite often grown as curiosities in hot houses in the more temperate regions. The size and structure of the inflorescence, the flower behavior, the short period of bloom, and the infrequency of bloom on these plants in cultivation create interest for both the casual observer and the scientist.

Few cytological observations have been reported for this entire genus of approximately 90 species. Stout (1937) reported observations on the pollen, the result of germination tests and the relation of the pollen tubes to the style for one plant of *A. titanum*. The writer knows of no report concerning the number of chromosomes in any plant of this genus.

Plants of two species of *Amorphophallus* have flowered in the conservatories of The New York Botanical Garden. A sixty-pound corm of *A. titanum* which was obtained by Dr. E. D. Merrill (1932) from A. M. Oostingh, Fort de Kock, Sumatra, in June, 1932, flowered in June 1937. An accurate description of the flowering of this corm was published in the Journal of The New York Botanical Garden (August 1937). Root tips were collected from the corm when it was removed from its tub three days after flowering. These root tips were not actively growing and none had mitotic figures.

Another smaller corm of *Amorphophallus titanum* was collected in Sumatra by Mr. B. A. Krukoff and sent to the Garden in 1935 (accession no. 77023). When the plant which was obtained from this corm was actively growing, root tips were collected and fixed for cytological observations. Later when the plant flowered in July 1939 it was identified as *A. titanum*. It was somewhat smaller than the plant which flowered in 1937.

The root tips were fixed in Flemming's medium fixative, sectioned, and stained with Heidenhain's hematoxylin. Each of the seventeen somatic cells in which the entire complement of chromosomes could be counted contained 26 chromosomes. A study of these showed that there were present 13 pairs of homologous chromosomes. It appears then that there were two sets of 13 chromosomes each. The members of one of these sets are shown in figure 1.

As shown, there were distinct differences in the size and shape of the chromosomes in each set. The longest chromosomes were about three times the length of the smaller ones. Since it was not convenient to make smear preparations of pollen-mother-cells the exact location of the spindle fiber

insertion regions was not determined. It seemed, however, that two of the chromosomes had median, four had submedian, and seven had terminal or sub-terminal insertion regions.

Plants of *Amorphophallus bulbifer* have been growing in the New York Botanical Garden greenhouses since 1902 when several corms were received from Edinburgh (accession no. 14468). Cytological studies of the root tips of a plant of *A. bulbifer* revealed that it had 36 chromosomes in its somatic cells. Study of these chromosomes seemed to indicate that each of the two sets of homologs was composed of 18 chromosomes which were somewhat morphologically different from one another. One set of 18 chromosomes is shown in figure 2. Only three chromosomes here designated B, O, and K, of *A. bulbifer*

1

2

FIG. 1. One set of chromosomes in the somatic tissue of *Amorphophallus titanum*.
FIG. 2. One set of chromosomes in the somatic tissue of *Amorphophallus bulbifer*.

appeared to be closely similar to chromosomes A, D, and K of *A. titanum*. All other chromosomes in a single set differed from one another as well as from all other chromosomes of *A. titanum*. Five of these chromosomes seemed to have median insertion regions, nine had sub-median and four had terminal or sub-terminal spindle fiber insertion areas.

Gaiser (1930) lists the number of chromosomes for 57 species of plants of the family Araceae. It is to be noted that *Arisaema serratum* var. *Thunbergii* f. *Blumei* is the only species for which the diploid number of 26 chromosomes is given. No species is accredited with 36 chromosomes in the somatic tissue. However, the 2n number of chromosomes in *Anthurium crassinervium* and *A. Wallisii* is ca. 60 and *A. radicans* is given as 50. The haploid number of 15 seems most frequent while 8, 9, 10, 12 and 16 have been observed in various species of the Araceae.

In this study it has been determined that for the plants studied the diploid number of chromosomes in somatic cells of *Amorphophallus titanum* is 26 and that for *A. bulbifer* is 36. Assuming that these are all in homologous pairs the haploid numbers for these plants are 13 and 18. And it is the giant species which has the lower number. These numbers do not indicate a simple polyploid relationship for these two species.

There is, however, a striking resemblance between chromosomes A and B; C and D; H, I, J and K; and M and N of a single set from *A. bulbifer* as may be observed in figure 2.

THE NEW YORK BOTANICAL GARDEN
NEW YORK

Literature Cited

Merrill, E. D. 1932. Sixty-pound corm received from Sumatra. Jour. N. Y. Bot. Gard. **33**: 155.

Gaiser, L. O. 1930. Chromosome numbers in Angiosperms II. Bibliographia Genetica **6**: 381–384.

Stout, A. B. 1937. Some observations on Flower Behavior in *Amorphophallus titanum*. Jour. N. Y. Bot. Gard. **38**: 197–200.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 615–628 NOVEMBER, 1943

THE GENUS STACHYURUS

HUI-LIN LI

In this study an attempt is made to summarize our present knowledge of the taxonomy of the genus *Stachyurus*, on the basis of the material available in the herbarium of the Arnold Arboretum of Harvard University. So complete is this material that only one recently described Japanese species, *S. ovalifolius* Nakai, has not been seen by this writer represented either by a type or a classical specimen. The types of the few varieties described in this paper are deposited in the herbarium of Arnold Arboretum.

Stachyurus was first described by Siebold and Zuccarini for *S. praecox*, a Japanese species, and included in the Pittosporaceae (Sieb. & Zucc. Fl. Jap. **1**: 43. 1835). Bentham (Jour. Linn. Soc. **5**: 55. 1861; Benth. & Hook. Gen. **1**: 184. 1862) later transfers it to the Ternstroemiaceae. To both of these families the genus is only remotely related. Gilg (in Engl. & Prantl, Nat. Pfl. **3** (6): 192. 1893) more appropriately creates for it the family Stachyuraceae and gives it a detailed treatment. Only two species were known at that time, namely, *S. praecox* Sieb. & Zucc. of Japan and *S. himalaicus* Hook. f. & Thomson of the Himalayan region. In the second edition of the Natürlichen Pflanzenfamilien (1925), the same treatment is reprinted without any additional data.

The forms treated in this review are all that are known at present, totaling twelve species and four varieties. The leaves are of special use in making taxonomic determinations. The shape, size, apex, base, margin, and venation of the leaves, as well as the length of the petioles, are used extensively to distinguish the different species. The length of the inflorescences, pedicels, and styles is also useful in identification. The flowering parts, except for minor points pertaining to the length of the styles, exhibit little variation. The size and shape of the fruit are sometimes essential for species identification.

Franchet (Jour. de Bot. **12**: 254. 1898) divides the genus into two sections, *Callosurus* and *Gymnosurus*. He characterizes the two sections as follows: "Sectio 1. Callosurus.—folia racemos axillentia persistentis; racemi pedunculati. Sectio 2. Gymnosurus.—folia racemos axillentia ante anthesim decidua; racemi sessiles." To the first section belong *S. yunnanensis* Franch. and *S. obovatus* (Rehder) Li, and to the second section the remaining species. The peduncles in the first section are rather short and not always distinct, but in the second section the inflorescences are invariably sessile or subsessile.

The inflorescences in both sections are spikes or racemes arising from the axils of leaves, usually produced by one-year-old wood. The differences that

Franchet emphasizes in his diagnostic summary are best interpreted as follows:

Sect. *Callosurus:* The spike grows on a normal axillary florescent axis, that is, without tending to displace or to suppress the leaf itself, and the leaf consequently persists throughout the flower- and fruit-stage.

Sect. *Gymnosurus:* The spike tends to eliminate the leaf, which is caducous; the result is that the inflorescences and infructescences are borne without a subtending leaf.

The basis of this difference, which Franchet fails to notice, is essentially physiological, and presumably, to a certain extent, also anatomical. In *Callosurus,* the part of the stem that bears the flowers and fruits remain essentially a vegetative axis with lateral inflorescences. In *Gymnosurus,* on the contrary, the same part of the stem tends to become a floriferous axis, in a manner suggestive of an apical or intercalary inflorescence. The passage from one form of habit to the other is subtle and may, in certain species, be apparent only as a tendency, but it is marked enough to justify the retention of Franchet's sections and characterizations.

Stachyurus is confined to the temperate regions of eastern Asia, extending from the eastern Himalayas in the west to the Bonin Islands in the east, but not ranging below 20° N. Lat. It is known in northern Burma, Tonkin, and Kwangtung proper, but apparently it is lacking in Hainan Island. On the Asiatic mainland, the spread of the genus scarcely extends northward to 35° N. Lat., but it is found in all parts of the Japanese Archipelago as far north as Hokkaido. The species are local in their distribution, except *S. praecox* Sieb. & Zucc., which is widely distributed in Japan proper, *S. chinensis* Franch. and its varieties, which are known in all the Chinese provinces where the genus is recorded, and *S. himalaicus* Hook. f. & Thomson, which extends from eastern India through southern China to Formosa.

STACHYURUS Sieb. & Zucc. Fl. Jap. **1**: 42. *pl. 18.* 1835; Endl. Gen. Pl. **2**: 1083 (n. 5669). 1840; Benth. & Hook. Gen. **1**: 194. 1862; Gilg in Engl. & Prantl, Nat. Pfl. **3** (6): 193. 1893; ed. 2. **21**: 458. 1925; Rehder, Man. Cult. Trees & Shrubs 640. 1927; ed. 2. 654. 1940.

Shrubs or small trees, deciduous or evergreen, glabrous, often with straggling branches, the branchlets with large pith, the winterbuds small, with 2–4 outer scales; leaves alternate, the petioles slender, the blades membranaceous to coriaceous, serrulate; stipules small, caducous; flowers small, regular, perfect or functionally dioecious, sessile to short-pedicellate, in erect or pendulous racemes or in spikes axillary on last years branches, with one bract at the base of the pedicel and two bracteoles subtending the flower; sepals and petals each four, free, imbricate; stamens 8, distinct, the anthers versatile; ovary superior, incompletely 4-celled by the intrusion of the parietal placentae, the style simple, short, the stigmas capitate, 4-lobed, the ovules many; fruit berry-like, with leathery pericarp; seeds many, small,

with soft arillus, albuminous, the embryo straight, the cotyledons elliptic, the radicles short.

TYPE SPECIES: *Stachyurus praecox* Sieb. & Zucc.

KEY TO THE SPECIES AND VARIETIES

A. Leaves at the base of the inflorescence persistent; inflorescences short-pedunculate. (Section I. *Callosurus* Franch.)

B. Leaves ovate to oblong-ovate; inflorescences 3–9 cm. long, with 12–22 flowers or fruits.

C. Fruits subsessile or very short pedicellate, the pedicels to 1 mm. long 1. *S. yunnanensis.*

CC. Fruits long-pedicellate, the pedicels 3–5 mm. long, articulate at the middle 1a. *S. yunnanensis* var. *pedicellatus.*

BB. Leaves obovate to oblong-obovate; inflorescences about 1.5 cm. long, with 3–8 (rarely 10) flowers or fruits 2. *S. obovatus.*

AA. Leaves at the base of the inflorescence early deciduous; inflorescences sessile or subsessile. (Section II. *Gymnosurus* Franch.)

B. Leaves oblong-lanceolate to linear-lanceolate, about 3 times or more as long as broad, the marginal teeth very fine, mostly close.

C. Leaves with longitudinal veins located a little more than half way between the midrib and margin, united with the straight or slightly curved lateral nerves.

D. Leaves narrowly linear-lanceolate, the base acute, the serrations more or less remote, inconspicuous, incurved and obtuse 3. *S. salicifolius.*

DD. Leaves oblong-lanceolate, the base cordate, the serrations fine, very close, more or less straight and pointed, rigid 4. *S. cordatulus.*

CC. Leaves without longitudinal veins, the lateral nerves ascending and prolonged.

D. Leaf-base acute, the apex acuminate, the marginal teeth sharp-pointed; petioles about 2.5 cm. long; inflorescences about 10 cm. long 5. *S. himalaicus.*

DD. Leaf-base cordate, the apex long-acuminate, the marginal teeth slightly incurved and obtuse; petioles about 4.5 cm. long; inflorescences about 14 cm. long 6. *S. lancifolius.*

BB. Leaves ovate-oblong to orbicular, about 2 times or less as long as broad, the marginal teeth coarse, generally more remote.

C. Leaves ovate-oblong, about 2 times as long as broad (Japanese species).

D. Leaves long-petiolate, the petioles 3–5 cm. long; fruits large, 1.3–2 cm. long.

E. Leaves long-acuminate, the base rounded to subcordate, the marginal teeth prominent, pointed; inflorescences robust, about 8–9 cm. long; fruits oblong-obovate, 1.3–5 cm. long 7. *S. Matsuzakii.*

EE. Leaves acute, the base broadly acute, the marginal teeth less prominent, obtuse; inflorescences slender, 4–5 cm. long; fruits broadly oblong, 1.8–2 cm. long.

F. Lateral nerves about 6 on each side 8. *S. macrocarpus.*

FF. Lateral nerves 9–11 on each side. 8a. *S. macrocarpus* var. *prunifolius.*

DD. Leaves with petioles about 1.5–2 cm. long; fruits small, about 1 cm. long 9. *S. praecox.*

CC. Leaves ovate to orbicular, as long as to less than 2 times as long as broad (Chinese species).

D. Leaves acuminate or cuspidate.

E. Leaves ovate, the apex long-acuminate, the base acute to rounded . . . . 10. *S. chinensis.*
EE. Leaves orbicular, the apex abruptly short-acuminate or cuspidate, the base cordate.
F. Leaves abruptly acuminate, the acumen 5–8 mm. long. 10a. *S. chinensis* var. *latus.*
FF. Leaves cuspidate-emarginate, the acumen 10–15 mm. long . 10b. *S. chinensis* var. *cuspidatus.*
DD. Leaves emarginate or bilobed . 11. *S. retusus.*
No specimen observed . . . 12. *S. ovalifolius.*

1. STACHYURUS YUNNANENSIS Franch. Jour. de Bot. **12**: 253. 1898; Rehder in Sarg. Pl. Wils. **1**: 288. 1912; Jour. Arnold Arb. **15**: 103. 1934; Chung, Mem. Sci. Soc. China **1**: 176. 1924; Hand.-Maz. Symb. Sin. **7**: 383. 1931. *Stachyurus Esquirolii* H. Lévl. Fl. Kouy-Tchéou 416. 1915. Figure 1.

A shrub, 1.5–3 m. tall, the branchlets olivaceous, with lenticels; leaves coriaceous, persistent, glabrous, greenish and slightly lustrous above, pale beneath, ovate-oblong to ovate-lanceolate, 6–12 cm. long, 2–4 cm. wide, the apex caudate-acuminate, the base acute, the margins finely and sharply serrulate, the teeth pointed, with callose apices, the lateral nerves 5–7 on each side, ascending, inconspicuous to subconspicuous above, slightly elevated and conspicuous beneath, the tertiary veins inconspicuous on both surfaces; petioles 1–2.5 cm. long; inflorescences 6–10 cm. long, erect or pendulous, short-pedunculate, the peduncles 0.5–1 cm. long, the flowers yellow, subsessile, the bracts triangular-ovate, acuminate, about 2.5 mm. long, the bracteoles ovate, acute, about 3 mm. long; sepals ovate, about 4.5 mm. long, acute; petals obovate, obtuse, 6–7 mm. long, about 4 mm. wide; filaments about 5 mm. long; ovary and style about 6 mm. long, scarcely exerted, the stigmas capitate, distinct; fruit globose, about 6 mm. across, sessile, with persistent style.

CHINA: SZECHUAN: Hung-yah Hsien, *E. H. Wilson 2555*; Ping-pien Hsien, *H. T. Tsai 62960*; Mt. Omei, *W. P. Fang 2634*, *T. T. Yu 399, 405*, *Y. S. Liu 1623, 1668, 1776*, *C. Y. Chiao & C. S. Fan 71, 235*, *K. N. Yin 138*. YUNNAN: Mo-so-yn (Lou Kong), *Delavay 822* (syntype, photo. and merotype of leaf in AA), April, 1884, *3334* (syntype, merotype of flowers in AA); Champutong, Der-la, *C. W. Wang 66805*. KWEICHOW: Than-lo, *J. Esquirol 3517* (holotype of *S. Esquirolii* H. Lévl., merotype in AA); An-lung, Kow-chang, *Y. Tsiang 7418*; Kweiyang, Chan Lin Shan, *S. W. Teng 90021*.

This species can be distinguished from the other two common Chinese species of the genus, *S. himalaicus* Hook. f. & Thomson and *S. chinensis* Franch., by the fact that the leaves at the base of the racemes are persistent rather than early deciduous. The leaves of *S. yunnanensis* resemble those of *S. himalaicus*, differing, in addition to the character mentioned above, in the generally smaller size and coarser and more remote serrations.

1a. STACHYURUS YUNNANENSIS Franch. var. PEDICELLATUS Rehder in Sarg. Pl. Wils. **1**: 288. 1912; Chung, Mem. Sci. Soc. China **1**: 176. 1924. Figure 2.

Differs from the species in the distinctly pedicellate fruit, the pedicels 3–5 mm. long, articulate at the middle.

CHINA: SZECHUAN: Yung-yang Hsien, *E. H Wilson 4541* (holotype) July, 1910. YUNNAN: Loping, Tjitjischan, *H. Handel-Mazzetti 27 = 10188* (immature fruits; identified by Handel-Mazzetti as *S. yunnanensis* Franch.).

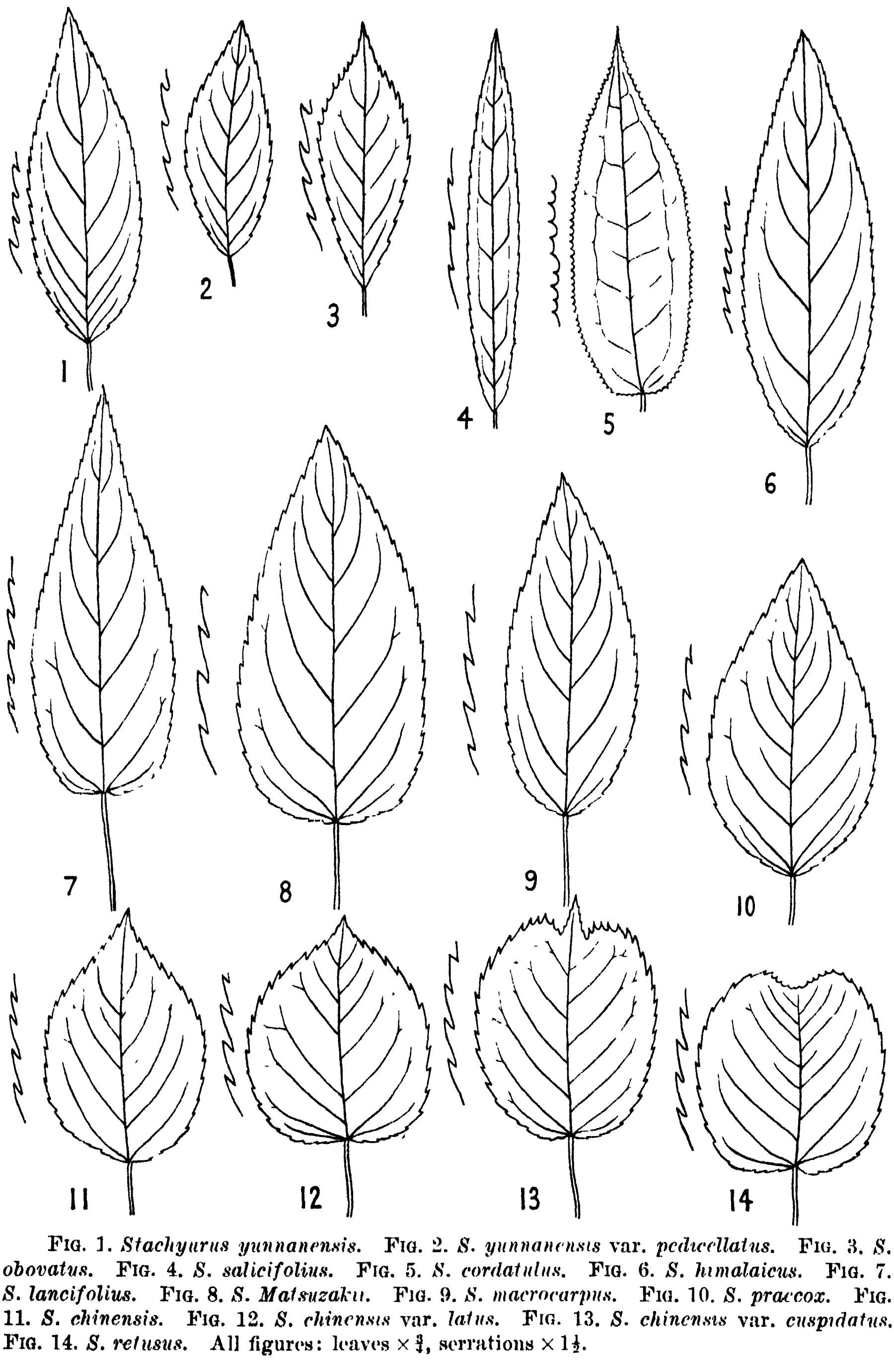


FIG. 1. *Stachyurus yunnanensis*. FIG. 2. *S. yunnanensis* var. *pedicellatus*. FIG. 3. *S. obovatus*. FIG. 4. *S. salicifolius*. FIG. 5. *S. cordatulus*. FIG. 6. *S. himalaicus*. FIG. 7. *S. lancifolius*. FIG. 8. *S. Matsuzakii*. FIG. 9. *S. macrocarpus*. FIG. 10. *S. praecox*. FIG. 11. *S. chinensis*. FIG. 12. *S. chinensis* var. *latus*. FIG. 13. *S. chinensis* var. *cuspidatus*. FIG. 14. *S. retusus*. All figures: leaves × $\frac{3}{4}$, serrations × $1\frac{1}{2}$.

2. **Stachyurus obovatus** (Rehder) Li, comb. nov. *Stachyurus yunnanensis* Franch. var. *obovata* Rehder in Jour. Arnold Arb. **11**: 165. 1930; Hand.-Maz. Symb. Sin. **7**: 383. 1931. Figure 3.

A shrub, 1–3 m. tall, the branchlets olivaceous; leaves subcoriaceous, persistent, short-petiolate, greenish and slightly lustrous above, pale beneath, obovate, 5.5–7.5 cm. long, 2–3 cm. wide, the apex long-caudate-acuminate, the acumen 1–1.5 cm. long, the base narrowly attenuate, the margins slightly serrulate to subentire below, finely and sharply serrulate above, the teeth pointed, slightly callose, the lateral nerves about 5–7 on each side, subconspicuous above, elevated and prominent beneath, the tertiary veins inconspicuous on both surfaces; petioles about 0.5 cm. long; inflorescences spicate, short-pedunculate, 1–1.5 cm. long, the flowers sessile to subsessile, the bracts ovate, long-acuminate, about 1.5 mm. long, the bracteoles ovate, about 2 mm. long; sepals ovate, about 2 mm. long; petals ovate, 4–5 mm. long, 2–5 mm. wide; filaments about 4 mm. long; ovary and style about 4 mm. long, included, the stigmas ovate; fruit globose, about 7 mm. across, pedicellate, the pedicels 3–4 mm. long, articulate at the middle.

CHINA: SZECHUAN: Kuan Hsien, *W. P. Fang 2000, 12156, F. T. Wang 20504, 20618, Y. S. Liu 1856, C. S. Fan 81;* Mt. Omei, *W. P. Fang 3910, 7833, 6158, Y. S. Liu 1725, C. Y. Chiao & C. S. Fan 412;* Ping-shan Hsien, *F. T. Wang 22698.*

Professor Rehder states that "this plant looks at the first glance very distinct on account of its obovate almost lyrate caudate-acuminate leaves, but the leaves of some specimens of *S. yunnanensis* before me show a tendency toward an obovate shape and the serration agrees with that of *S. yunnanensis.* As the flowers are unknown, the specimens bearing young fruits, it does not seem wise to describe it as a new species." With adequate flowering material (*Fang 12156* and *Wang 22698*) and young fruiting material (*Wang 20504, 20618*) on hand, this writer is convinced that the variety deserves a specific standing. The leaves are not only distinctly and constantly obovate in shape, but they are also generally smaller than those of *S. yunnanensis* Franch. Moreover, the inflorescences are characteristically very short, scarcely exceeding 2 cm. long, and bearing only 3–8, rarely 10, flowers or fruits, and the styles are included, while in *S. yunnanensis* the inflorescences are 3–9 cm. long, bearing 12–22 flowers or fruits, and the styles are exerted.

3. STACHYURUS SALICIFOLIUS Franch. Jour. de Bot. **12**: 253. 1898; Chung, Mem. Sci. Soc. China **1**: 176. 1924. Figure 4.

A shrub, 1.5–3 m. tall, the branchlets olivaceous, glabrous; leaves chartaceous, glabrous, dark green above, pale beneath, linear-lanceolate, 8–15 cm. long, 0.7–1.7 cm. wide, the apex caudate-acuminate, the base obtuse, the margins inconspicuously serrulate, the teeth obtuse, incurved, the lateral nerves about 6–8 on each side, at first obliquely spreading, then abruptly ascending into longitudinal veins parallel to the midrib, their tips frequently joining the preceding lateral nerves, inconspicuous above, slightly elevated and conspicuous beneath, the tertiary veins inconspicuous on both surfaces; petioles short, 4–8 mm. long; inflorescences 5–7 cm. long, erect or pendulous, subsessile; flowers greenish white, subsessile or short-pedicellate, the bracts triangular-ovate, acuminate, about 2 mm. long, the bracteoles ovate, acute, about 2.5 mm. long; sepals ovate, about 4 mm. long, acute; petals obovate,

about 4 mm. long, 3–5.5 mm. wide, obtuse; filaments 5–6 mm. long; ovary and style about 6 mm. long, scarcely exerted, the stigmas capitate, distinct; fruit globose, about 4–6 mm. in diameter, with persistent style, the pedicels about 2.5 mm. long.

CHINA: SZECHUAN: Mt. Omei, *E. H. Wilson 4808*, *W. P. Fang 2720, 3186, 12890*, *T. T. Yü 409, 452*, *Y. S. Lau 1142*; Ping-shan Hsien, *F. T. Wang 22752, 22763*. YUNNAN: Tschen-fong shan, *R. P. Delavay s.n.* (holotype, photo. and merotype in AA), July, 1894; Yi-liang Hsien, *H. T. Tsai 52118*.

This species is easily distinguished from the others by the long and narrow linear-lanceolate leaves with rather short petioles 4–5 mm. long.

4. **Stachyurus cordatulus** Merr. Brittonia **4**: 122. 1941. Figure 5.
A shrub, subscandent, the branches glabrous; leaves chartaceous to coriaceous, glabrous, olivaceous on both surfaces to slightly paler beneath, oblong to oblong-lanceolate, 10–12 cm. long, 2.3–4 cm. wide, the apex subcaudately acuminate, the base slightly or distinctly cordate, the margins finely and sharply serrulate, the teeth pointed, spreading, about 0.5 mm. long, with callose apices, the lateral nerves 7 or 8 on each side, spreading, straight or slightly curved, united with longitudinal nerves located a little more than half way between the midrib and the leaf margins, subconspicuous above, distinct and elevated beneath, the tertiary veins inconspicuous on both surfaces; petioles 6–9 mm. long; inflorescences spicate, 4–9 cm. long, subsessile, the flowers greenish to slightly rosy, 5–6 mm. long, sessile, the bracts 1.5–2 mm. long, ovate at base, long-acuminate, the bracteoles ovate, about 2 mm. long, subacute to short-acuminate; sepals elliptic, concave, rounded, about 3 mm. long; petals obovate, rounded, about 5 mm. long and 3.5 mm. wide; filaments 1.5–2 mm. long; ovary ovoid, the style about 1 mm. long, the stigmas capitate, about 1 mm. in diameter.

BURMA: 'Nam Tamai at the Adung-Sienghku confluence, and along the Adung River, *K. F. Ward 9176* (paratype), *9191* (holotype), Jan. and Feb., 1931.

This distinct species is near to *Stachyurus himalaicus* Hook. f. & Thomson in the oblong-lanceolate leaves with fine and close serrations, but it is easily distinguished from the latter in that its leaves are shorter-petiolate, the base more distinctly cordate, the apex longer-acuminate, and the serrations straight, out-pointed, and more rigid. Moreover, the species is characterized by the venation, the straight or slightly curved lateral nerves being united directly with the nearly as prominent longitudinal pair, which is located a little more than half way between the midrib and the leaf-margins. A similar characteristic venation is found only in *S. salicifolius* Franch., but in that case the longitudinal veins are not always as distinct and sometimes are represented by extensions of the lower lateral veins not fully connected with the upper lateral ones. In other respects, *S. salicifolius* is readily distinguished from *S. cordatulus* by its very narrow linear-lanceolate leaves with acute bases and remote, obscure, and obtuse serrations.

5. **Stachyurus himalaicus** Hook. f. & Thomson ex Benth. Jour. Linn. Soc. Bot. **5**: 55. 1861; Thiselton-Dyer in Hook. f. Fl. Brit. Ind. **1**: 288. 1875; Rehder in Sarg. Pl. Wils. **1**: 287. 1912; Hayata, Ic. Pl. Formosan. **5**: 8. *f. 3.*

1915; Kanehira, Formosan Trees 62. *f.* 1917; Chung, Mem. Sci. Soc. China **1**: 176. 1924; Ito, Taiwan Shokubutu Dzusetu (Ill. Formosan Pl.) *pl. 464.* 1927; Chun, Sunyatsenia **1**: 275. 1934; Merr. Brittonia **4**: 121. 1941. *Stachyurus Sigeyosii* Masamune, Trans. Nat. Hist. Soc. Formosa **28**: 287. 1938, syn. nov. Figure 6.

A small tree with spreading branches, the branchlets chestnut-brown, with whitish lenticels; leaves chartaceous to coriaceous, glabrous, greenish above, pale beneath, oblong to oblong-lanceolate, 8–13 cm. long, 3.5–5.5 cm. wide, the apex long-caudate-acuminate, the base rounded to subcordate, the margins finely serrulate, the teeth minute, pointed, with callose apices, the lateral veins 5–7 on each side, ascending, elevated and prominent on both surfaces, the tertiary veins reticulate, subconspicuous on both surfaces; petioles 0.5–1.5 cm. long; inflorescences 5–10 cm. long, erect or pendulous, sessile, the flowers yellow, sessile, the bracts triangular-ovate, acuminate, about 2 mm. long, the bracteoles broadly ovate, acute, about 2 mm. long; sepals broadly ovate, obtuse, about 3 mm. long; petals obovate, rounded, 5 mm. long, 3.5 mm. wide; filaments 4–5 mm. long; ovary and style about 5 mm. long, scarcely exerted, the stigmas capitate; fruit subglobose, about 7–8 mm. across, subsessile to short-pedicellate, with short persistent style, the pedicels 2–3.5 mm. long, articulate at the middle.

CHINA: HUNAN: Sinning Hsien, *C. S. Fan & Y. Y. Li 608.* HUPEH: Chang-yang Hsien, *E. H. Wilson 192a;* no precise locality, *A. Henry 3449 A* (fragmentary). SZECHUAN: Mt. Omei, *Y. S. Liu 1670, C. Y. Chiao & C. S. Fan 387;* Kuan Hsien, Chien-chang Shan, *C. S. Fan 15.* SIKANG: Ya-an, *C. Y. Chiao 1925.* YUNNAN: no precise locality, *E. E. Maire 68, G. Forrest 9522, 9776, 16213, T. T. Yu 11434, H. T. Tsai 57266, 57599;* Mengtze, *A. Henry 10138, 10138A, 10543;* Niou-lou-kiang, *E. E. Maire 83;* between Schinlung and Ta Sung Shu, *C. Schneider 313;* Yunnanfu, *C. Schneider 378;* Ta Chang, *C. Schneider 749;* Likiang, *C. Schneider 2841, J. F. Rock 10575, G. Forrest 22221, C. W. Wang 70699, K. M. Feng 404, R. C. Ching 21595;* Tengyueh, *J. F. Rock 7994;* Champutong, Mt. Kenyichunpo, *J. F. Rock 11525;* Pe Yen Tsin, Son Pin Chao, *S. Ten 354, 364;* Ma-kwan Hsien, *H. T. Tsai 51851;* Shang-pa Hsien, *H. T. Tsai 54738;* Lan ping Hsien, *H. T. Tsai 54047, 56283;* Lung-ling Hsien, *H. T. Tsai 56461;* Wei-si Hsien, *H. T. Tsai 63019, C. W. Wang 67900;* Champutong, *C. W. Wang 66709;* Kiukiang Valley, *T. T. Yu 19438;* Londjrela, *T. T. Yu 23147;* northern flank of Haba Snow Range, *K. M. Feng 1184;* southern Chungtien, *K. M. Feng 3087.* KWEICHOW: Fan Ching Shan, *Steward, Chiao, & Cheo 28.* KWANGSI: Ling-wan Hsien, *S. K. Lau 20458, Steward & Cheo 625;* Kwei-lin Hsien, Ma-wang-shan, *W. T. Tsang 28230, 28349.* KWANGTUNG: Pan Ling Tsze, *W. Y. Chun 5880;* Yang Shan Hsien, *T. M. Tsiu 741;* Loh chang Hsien, Chong Uen Shan, *W. T. Tsang 20713, 20674.*

FORMOSA: No precise locality, *J. L. Gressitt 116;* Kuanania, *O. Warburg 10479;* Arisan, prov. Kagi, *E. H. Wilson 9752, 10799;* Horisha, prov. Nanto, *E. H. Wilson 10097;* Taiheisan, prov. Giran, *E. H. Wilson 10175, S. Suzuki s.n., K. Uno 10674;* Bankingin, *A. Henry 35;* Hassensan, *R. Kanehira 21190;* Sankyo, *K. Odashima 17850.*

INDIA: Eastern Himalaya, *K. Biswas s.n.*

BURMA: Above Zuklang, *F. K. Ward 427;* Adung Valley, *K. F. Ward 9297.*

This widely distributed species can be distinguished from *S. chinensis* Franch., another species of very wide distribution, by its longer but narrower, oblong or oblong-lanceolate leaves with fine and close serrations, and by the smaller flowers with the style scarcely exceeding the petals. Its inflorescence is also generally much longer. This writer has not been able to distinguish the Formosan *S. Siegeyosii* Masamune by its descriptions from

S. himalaicus especially from the Formosan plants of the latter species, and thus treats the former as a synonym of the latter.

6. STACHYURUS LANCIFOLIUS Koidz. Bot. Mag. Tokyo **32**: 135. 1918. *Stachyurus praecox* sensu Ito & Matsum. Tent. Fl. Lutch. **1**: 60. 1899, non Sieb & Zucc. Figure 7.

A shrub, 1.5–2.5 m. tall, the branchlets dark chestnut-brown, glabrous; leaves chartaceous, glabrous, lanceolate to ovate-lanceolate, rarely ovate-oblong, 12–19 cm. long, 3.5–7.5 cm. wide, the apex long-caudate-acuminate, the base rounded to subcordate, the margins finely serrulate, the teeth slightly incurved, obtuse, the lateral veins about 8 on each side, ascending, subconspicuous above, elevated and prominent beneath, the tertiary veins reticulate, inconspicuous above, subconspicuous beneath; petioles 3–5 cm. long; inflorescences 5–10 cm. long, sessile, pendulous, the flowers pale yellow, sessile, the bracts triangular-ovate, about 2 mm. long, acuminate, the bracteoles ovate, about 3 mm. long, obtuse; sepals ovate, about 4 mm. long; petals obovate to suborbicular, about 6–7 mm. long, 5–6 mm. wide, the apex rounded; filaments 3.5–4.5 mm. long; ovary and style about 3 mm. long, the stigmas capitate, distinct; fruit ellipsoidal, 9–12 mm. long, short-pedicellate.

JAPAN: Kyushu, *E. H. Wilson s.n.*, 3 collections; Liukiu Islands, *Yokohama Nursery Co., s.n.*

This species is close to *Stachyurus himalaicus* Hook. f. & Thomson in the oblong- or ovate-lanceolate finely serrulate leaves with rounded to subcordate bases, but differs in the longer petioles, slightly larger and more obtuse serrations, longer inflorescences with larger and more densely arranged flowers, and the larger fruits. The type is described from Kyushu, Japan, but no specimen is cited in the original description.

7. STACHYURUS MATSUZAKII Nakai, Bot. Mag. Tokyo **34**: 146. 1920. Figure 8.

A shrub about 5 m. tall, the branchlets stout, chestnut-brown dotted with white lenticels; leaves chartaceous, glabrous, greenish above, pale beneath, elliptic, 10–14 cm. long, 5–6.5 cm. wide, the apex long-acuminate, the base acute to rounded, the margins coarsely and prominently serrulate, the teeth large, obtuse, slightly incurved, with callose apices, the lateral nerves 5 or 6 on each side, ascending, subconspicuous above, elevated and prominent beneath, the tertiary veins reticulate, inconspicuous above, slightly conspicuous beneath; petioles 2.5–5 cm. long; inflorescences 4–12 cm. long, sessile, pendulous, the flowers sessile, light yellow, the bracts broadly triangular-ovate, about 2.5 cm. long, acuminate, the bracteoles ovate, about 3 mm. long, acute to obtuse; sepals ovate, about 3 mm. long, acute; petals 5–7 mm. long; fruits obovate-oblong, 13–15 mm. long, with short persistent styles.

JAPAN: Hondo, Shima, *Soemjima 9228*.

This species is characterized by its rather robust branches, long-petiolate and large leaves, which are coarsely serrulate, and the rather stout inflorescences. Two type collections are cited by Nakai, both from prov. Idzu, Hondo, the first from Hachijo Isnad, *T. Nakai & N. Matsuzakii s.n.*, and another from Oshima Island, *Saburo Okubo s.n.*

8. STACHYURUS MACROCARPUS Koidz. Bot. Mag. Tokyo **32**: 134. 1918. Figure 9.

A shrub, the branchlets dark chestnut-brown to blackish, glabrous; leaves chartaceous, glabrous and greenish above, pale beneath and slightly pubescent along the midrib and lateral nerves, soon glabrous, oblong to oblong-lanceolate, rarely ovate-elliptic to ovate-oblong, 7–14 cm. long, 3–5.5 cm. wide, the apex acuminate, the base rounded to obtuse, the margins obtusely and rather broadly serrulate, the teeth slightly incurved, with callose apices, the lateral nerves about 6 on each side, ascending, subconspicuous above, elevated and distinct beneath, the tertiary veins reticulate, inconspicuous above, subconspicuous beneath; petioles 2–5 cm. long; inflorescences 3.5–4 cm. long, subsessile, the flowers subsessile, rather densely arranged, the bracts broadly triangular-ovate, about 2 mm. long, acuminate, the bracteoles ovate, obtuse, about 2.5 mm. long; sepals ovate, about 3 mm. long; petals obovate, obtuse, about 5 mm. long and 3 mm. wide; filaments about 4 mm. long; ovary and style about 4 mm. long, the stigmas capitate, distinct; fruit oblong, 18–20 mm. long, 12–16 mm. wide, subsessile.

BONIN ISLANDS: No precise locality, *Hidemasa Otorno s.n.*, 2 collections.

This species is characterized by its oblong to oblong-lanceolate and acuminate leaves with remote and obtuse serrations, rather short inflorescences about 3.5–4 cm. long, and large fruits up to 2 cm. long. The type specimen is *S. Nishimura 105* from Chichishima Island, Bonin.

8a. STACHYURUS MACROCARPUS Koidz. var. PRUNIFOLIUS Tuyama, Bot. Mag. Tokyo **53**: 7, (as *purnifolius*). 1939.

Differs from the species in the thinner leaves with smaller, closer, acute serrations, and more numerous lateral nerves, about 9–11 on each side.

Recorded by T. Tuyama from Bonin Islands (type specimen: Hahazima Island, *T. Tuyama s.n.*); no specimen seen by this writer.

9. STACHYURUS PRAECOX Sieb. & Zucc. Fl. Japon. **43**: *pl.* 18. 1835; Abh. Math.-Phys. Cl. Bayer. Akad. Wiss. **4** (2): 152. 1845; Franch. & Sav. Enum. Fl. Jap. **1**: 59. 1875; Carrière, Rev. Hort. **1869**: 200. *f. 19.* 1869; Rouhard, Rev. Hort. **1908**: 86. *f. 28, 29.* 1908; Hook. Bot. Mag. **108**: *pl. 6631.* 1882; K. Ito, Fig. & Descr. Pl. Koishik. Bot. Gard. **2**: *pl. 22.* 1883; Lauche, Deutche Dendrol. ed. 2: 413. *f. 163.* 1883; Nicholson, Ill. Dict. Gard. 3: 483. *f. 518.* 1887; Bull. Coll. Agric. Tokyo **2**: *pl. 7, f. 21.* 1895; Gard. Chron. III. **21**: *f. 97.* 1897; Shirasawa, Ic. Ess. Forest Jap. **1**: *pl. 74.* 1900; Schneider, Dendrol. Winterst. 86. *f.* 1903; Ill. Hand. Laubh. **2**: 363. *f. 244a–b, 245.* 1909; Dallimore, Gard. Chron. III. **43**: 196. *f. 83.* 1908, 49: 213. 1911; Miyoshi, Pl. World. Jap. 128: *f.* 1917; Osborn, Garden **75**: 204. *f.* 1911; Gard. Chron. III. **79**: 229. 1926; Bean, Trees & Shrubs **2**: 545. *f.* 1914; Rehder in Bailey, Stand. Cycl. Hort. **6**: 3221. *f. 3674.* 1917; Man. Cult. Trees & Shrubs 640. 1927; ed. 2, 654. 1940. *Stachyurus japonicus* Steud. Nom. ed. 2, **2**: 630. 1841, sphalm. Figure 10.

A shrub, 1–4 m. tall, the branches spreading, the branchlets reddish brown or chestnut-brown, lustrous, glabrous; leaves chartaceous, greenish, lustrous and glabrous above, pale and slightly pubescent along the midrib and lateral nerves beneath, soon glabrous, elliptic-ovate to ovate-lanceolate, 7–15 cm.

long, 3.5–6.5 cm. wide, the apex long-acuminate, the base rounded to subcordate, the margins serrulate, the teeth slightly spreading, the lateral nerves about 5 or 6 on each side, ascending, more or less elevated and prominent on both surfaces; petioles 2–5 cm. long; inflorescences 5–9 cm. long, sessile to subsessile, erect or pendulous, the flowers yellow, sessile, the bracts broadly ovate, acute, about 2 mm. long, the bracteoles broadly ovate, obtuse, about 2 mm. long; sepals broadly ovate, acute, about 3 mm. long; petals obovate, 6–7 mm. long, 4–5 mm. wide; filaments 4–5 mm. long; ovary and style 4–5 mm. long, included, the stigmas capitate, distinct; fruit globose, about 8 mm. long, with or without persistent styles, short-pedicellate, the pedicels 1.5–2 mm. long, articulate at the middle.

JAPAN: No precise locality, *Faurie 6128*, *H. Kuenberg 2840a*; Hokkaido, prov. Oshima, *K. Miyabe & Y. Tokubuchi s.n.*; Hokkaido, *C. S. Sargent s.n.*; Hokkaido, Kakkumi Hot Spring, *C. S. Sargent s.n.*; Atami to Odawara, *C. S. Sargent s.n.*; Miyanoshita, *C. S. Sargent s.n.*; Hondo, Shinano prov., *E. H. Wilson s.n.*; Hondo, Safami prov., *E. H. Wilson s.n.*; Hondo, Mino prov., *K. Shiota 310, 8055, 9683*; Kyushu, Nagasaki, *E. H. Wilson s.n.*; Kyushu, Mt. Kirishima, *E. H. Wilson s.n.*; Nokogiriyama, prov. Awa, *K. Miyabe s.n.*; Chikugo, *H. Mayr s.n.*; Nikko, *N. Mochizuki s.n.*; Mt. Amgi, *Sci. Coll. Imp. Univ. s.n.*; Iyo, *K. Sakurai s.n.*; between Shojiko and Kofu, *P. H. Dorsett & W. J. Morse 561*, Kobe, Rokkosan, *K. Uno 13656*; Ikerigaseki, Aomoriken, *K. Uno 2597*.

A species of common and wide occurrence in Japan, now frequently cultivated for its flowers. Siebold and Zuccarini, in their original description of the genus and the species, mention that the plant is common in Japan, but cite no specimen.

10. STACHYURUS CHINENSIS Franch. Jour. de Bot. **12**: 254. 1898; Diels, Bot. Jahrb. **92**: 475. 1900; Lecomte, Fl. Gén. Indo-Chine **1**: 353. *f. 33, 12–18.* 1910; Rehder in Sarg. Pl. Wils. **1**: 287. 1912; in Bailey, Stand. Cycl. Hort. 6: 3221. 1917; Jour. Arnold Arb. **8**: 178. 1927; Man. Cult. Trees & Shrubs 641. 1927; ed. 2, 654. 1940; Bean, Gard. Chron. III. **58**: 147. *f. 47.* 1915; Garden **79**: 182 *f.* 1915; Bowles, Garden **82**: 161. *f.* 1918; Chung, Mem. Sci. Soc. China **1**: 176. 1924; Osborn, Gard. Chron. III. **79**: 229. *f. 113.* 1926; Kirk, Brit. Gard. Flora 129. *f. 45.* 1927; Merr. Lingnan Sci. Jour. **7**: 316. 1931; Hand.-Maz. Symb. Sin. **7**: 383. 1931; Ganteau, Rev. Hort. **1932**: 95. *f. 33.* 1932. *Stachyurus praecox* sensu Diels, Bot. Jahrb. **29**: 475. 1900, non Sieb. & Zucc. *Stachyurus Duclouxii* Pitard ex Chung, Mem. Sci. Soc. China **1**: 176. 1924, nomem nudum, syn. nov. Figure 11.

A shrub, 3–5 m. tall, the branchlets dull brownish, with scattered whitish lenticels, glabrous; leaves chartaceous to membranaceous, greenish and glabrous above, pale and glabrous and slightly pubescent along the midrib and lateral nerves beneath, soon glabrous, ovate to ovate-oblong, 6–12 cm. long, 2.5–7.5 cm. wide, the apex more or less abruptly long-acuminate, the base rounded to subcordate, the margins crenate-serrulate, the lateral nerves 5 or 6 on each side, elevated and conspicuous on both surfaces, the tertiary veins reticulate, subconspicuous to conspicuous on both surfaces; petioles 1–2 cm. long; inflorescences 6–13 cm. long, sessile, the flowers yellow, subsessile or short-pedicellate, the bracts triangular-ovate, acuminate, about 2.5 mm. long, the bracteoles ovate, acute, about 3 mm. long; sepals ovate, obtuse, about 3.5 mm. long; ovary and style 6–7 mm. long, exerting the

petals, the stigmas capitate, distinct; fruit globose, about 6 mm. in diameter, with or without persistent styles, short-pedicellate, the pedicels about 1.5 mm. long.

CHINA: HUNAN: Hsinhwa, Hsikwanshan, *H. Handel-Mazzetti 582=11763;* Yi-chang Hsien, Ping Ton Shan, *W. T. Tsang 23528.* HUPEH: no precise locality, *A. Henry s.n.;* Ichang, *E. H. Wilson 89, 125;* Chang-yang Hsien, *E. H. Wilson 192;* Hsing-shan Hsien, *E. H. Wilson 2556;* Gian Gia-kou, *W. Y. Chun 3585;* Tan Shu Ya, *W. Y. Chun 4408;* Siu Jeh-su, *W. Y. Chun 4415;* Patung Hsien, *H. C. Chow 63.* SZECHUAN: No precise locality, *A. Henry 5744;* Chung-hsien, *W. P. Fang 506;* Nanchuan Hsien, *C. Bock & A. Rosthorn 2000, W. P. Fang 1064;* Kuan Hsien, *W. P. Fang 2211, S. S. Chien 5117, F. T. Wang 20496, 20583;* Lishui Hsien, *W. P. Fang 20;* Opien Hsien, *W. P. Fang 7238, Y. S. Liu 1999;* Mt. Omei, *W. P. Fang 2392, 2466, 2589, 3042, 3207, F. T. Wang 23219a, Y. S. Liu 1207, T. T. Yü 386, 448, S. S. Chien 5543;* Hung-ya Hsien, *W. P. Fang 7977, 8117, 8518, 8636;* Ma-pien Hsien, *W. P. Fang 4607;* Chenk-kou Hsien, *W. P. Fang, 10049;* Han-yuan, *W. C. Cheng 649, 669;* Mao Hsien, *F. T. Wang 21943;* Kwang-yun Hsien, *F. T. Wang 22638;* Ping-shan Hsien, *F. T. Wang 22703;* Ma-pien Hsien, *F. T. Wang 22857;* Lololand, between Alami and Ssuqueh, *C. Schneider 927;* between Oti and Quentin, *C. Schneider 1389.* SIKANG: Dzer-nar, Tsa-wa-rung, *C. W. Wang 66318, 66356, 66389, 66392;* Kanting, near Wu Ya Ling, *C. Y. Chiao 1741.* YUNNAN: No precise locality, *G. Forrest 10143, 10245, H. T. Tsai 57320, T. T. Yü 10259;* Longki and Tchan-fong-shan, *R. P. Delavay s.n.* (holotype, photo. and merotype in AA); Suen-oui, *E. E. Maire 79;* Cai-pou, *E. E. Maire 146;* Likiang, *C. Schneider 2930, 3498, J. F. Rock 4059, 8059, 8541;* Chao-tung Hsien, *H. T. Tsai 50899;* Cheng-hsiung Hsien, *H. T. Tsai 52305;* Ping-pien Hsien, *H. T. Tsai 62297, 62613;* Shang-pa Hsien, *H. T. Tsai 54805, 59103, 56542;* Chi-tze-lo, *H. T. Tsai 54189, 58558;* Wei-si Hsien, *C. W. Wang 63031, 63589, 63694, 64055, 68084;* Champutong, *C. W. Wang 66682;* Atungtze, Mt. Kakerpu, *T. T. Yu 10322;* Shunning, Hila, *T. T. Yü 16474;* southern Chungtien, Anangu, *K. M. Feng 1011.* KWEICHOW: Tsungyi Hsien, *Steward, Chiao, & Cheo 32;* Kweiyang, *S. W. Teng 90041.* KWANGSI: Northern Luchen, Chufeng-shan, *R. C. Ching 5782;* northern Hin Yen, Yeo Mar Shan, *R. C. Ching 7154;* Chuen Yuen, *Z. S. Chung 82022.* KWANGTUNG: Lohchang Hsien, *Y. Tsiang 1373, 1399;* Yu-yuen, *S. P. Ko 9192, 52562.* FUKIEN: No precise locality, *Hongk. Herb. 2403;* Pu-cheng, *R. C. Ching 2503.* (Also recorded from Shensi, Anhwei, Chekiang, and Kiangsi (Rehder l.c., Merrill, l.c.).

INDO-CHINA: Tonkin, Chapa, *A. Petelot 5690.*

This species of very wide distribution is close to the common Japanese species *S. praecox* Sieb. & Zucc., but may be distinguished by the broader and more abruptly acuminate leaves, the relatively longer petioles, the shorter pedicels in the fruit, and the smaller fruit. The leaves of *S. praecox* are more oblong and longer acuminate.

A photograph taken by Professor Rehder from the type specimen of *Stachyurus Duclouxii* C. J. Pitard in the Paris Museum (Yunnan: Hay tien, *Fr. Ducloux 2367*, March, 1904), which apparently has never been published, together with fragments of leaves and inflorescences, are found in the herbarium of the Arnold Arboretum. The name is listed in Chung's Catalogue of Trees and Shrubs of China (l.c.), probably being based on this particular photograph. The specimen is a flowering plant with juvenile leaves. It apparently represents *S. chinensis* Franch.

Stachyurus chinensis is quite variable in the size, shape, and serration of the leaves. These variations, however, although manifest in some cases, are gradual and inconstant. The species as a whole is generally easily recognizable and distinguishable from other species. The following varieties are recognized.

10a. STACHYURUS CHINENSIS Franch. var. **latus** Li, var. nov. Figure 12.

A typo speciei differt foliis plerumque latioribus, tenuiorbius, 6–7.5 cm. longis, 5–6.5 cm. latis, suborbicularibus vel ovatis, basi distincte cordatis, margine crasse serrulatis, apice abrupte acuminatis, acumine 5–8 mm. longo.

CHINA: ANHWEI: Chiuhwashan, *S. C. Sun, 1216.* HONAN: Sunghsien, San Kuan Miao, *J. Hers 1305* (TYPE), Sept., 1919. HUPEH: Feng Hsien, *E. H. Wilson 292;* Wan Tsao Shan, *W. Y. Chun 3901, 3956;* Hsin Tien Tsze, *W. Y. Chun 4039, 4011;* Huan Tsao, *W. Y. Chun 1138.* SZECHUAN: Nanchuan Hsien, *C. Y. Hwang 99, W. P. Fang 830, 920, 1024, 1402, 5528;* Cheng-kou Hsien, *W. P. Fang 10309.*

This variety is found in the provinces along the Yangtze Valley and north of it. The typical form of the species is found mainly in the southern provinces. The Honan and Anhwei specimens of this variety are clearly different from the typical form, while plants from western Hupeh and Szechuan, where the typical form is also located, are in some instances without very sharp distinction. The typical form, occurring in the south, is nearer to *S. himalaicus* Hook. f. & Thomson both geographically and structurally in the shape and serrations of the leaves than this variety.

It could be mentioned in this connection that specialization in the shape and serrations of the leaves in the genus is clearly traceable, as illustrated by the figures, from *S. himalaicus,* with oblong-ovate, acuminate, finely serrulate leaves, to *S. chinensis,* then to *S. chinensis* var. *latus* and *S. chinensis* var. *cuspidatus,* finally to *S. retusus,* with orbicular, emarginate, cordate leaves with much coarser serrations.

10b. STACHYURUS CHINENSIS var. **cuspidatus** Li, var. nov. Figure 13.

A typo speciei differt foliis suborbicularibus, 6.5–7.5 cm. longis, 5.5–6.5 cm. latis, basi rotundatis vel cordatis, apice latis, cuspidato-emarginatis, acumine lineari, 1–1.5 cm. longo, 0.3–0.5 cm. lato, interdum nullo.

CHINA: SZECHUAN: West of Wen-chuan Hsien, *W. P. Fang 20945* (TYPE), May 21, 1931.

11. STACHYURUS RETUSUS Yang, Contr. Biol. Lab. Sci. China **12**: 105. *pl. 6.* 1939. Figure 14.

A shrub, about 3 m. tall, the branchlets dark olivaceous, covered sparsely with white lenticels; leaves chartaceous, green, lustrous, and glabrous above, pale, white, tomentose to glabrous beneath, orbicular-oblong, 4.5–8 cm. long, 4–8 cm. wide, the apex retuse, rarely truncate or bilobed, the base cordate, the margins serrulate, the teeth obtuse, slightly incurved, the lateral nerves 5 or 6 on each side, ascending, elevated and prominent on both surfaces, the tertiary veins reticulate, conspicuous on both surfaces; petioles 1.5–2.3 cm. long; inflorescences (immature) to 4 cm. long, pendulous, subsessile, the bracts broadly triangular-ovate, about 2 mm. long, acuminate, the bracteoles 2, the flower buds sessile, the style very short, the stigmas globose, 4-lobed.

CHINA: SZECHUAN: Mt. Omei, *F. T. Wang 23248.*

This species is characterized by its suborbicular leaves, which are emarginate or bilobed at the apex and cordate at the base. Yang, basing on *C. W. Yao 3365* from Mt. Omei, Szechuan, describes the lower surface of the leaves as being densely covered with white hairs, which are not observed in the

above cited specimen, but which may be present on younger specimens and falling off in age as in some other species of the genus. The specimen cited, collected from the type locality, bears also immature racemes like the type and therefore no additional data could be added. The leaves are more or less chartaceous, in size and serration closely resembling those of *S. chinensis;* the general shape resembles especially that of var. *latus*. Apparently the leaf represents further specialization resulting in the disappearance of the acumen of var. *cuspidatus*. Occasionally an emarginate leaf like that of this species can also be found on a few specimens of *S. chinensis*. More material, particularly mature flowering and fruiting specimens, is needed for study in order to decide whether it is best to treat this as a variety of *S. chinensis* or to retain it as specifically distinct from the latter.

12. STACHYURUS OVALIFOLIUS Nakai, Jour. Jap. Bot. **15**: 534. 1939.

A shrub, 3–6 m. tall, the branches pale brownish to red-brownish; leaves ovate to broadly ovate to cordate-ovate, green and glabrous above, pale and sparsely pilose along the nerves or glabrous beneath, 7–12 cm. long, 5–7 cm. wide, the apex cuspidate, the base rounded or cordate to truncate, the margins coarsely mucronate-serrulate; petioles 1–5 cm. long; inflorescences racemose, dioecious, the male 7–12 cm. long, the female 3–7 cm. long, glabrous, the bracts deciduous; sepals and petals 4, distinctly imbricate; stamens 8, in 2 series, in male flowers 6–7 mm. long, in female flowers 3 mm. long, the anthers ovate-rounded; ovary ovate, the base pilose, the style 2–2.5 mm. long, the stigmas capitate; fruits about 15 mm. long, oblong to oblong-pyriform, with persistent style.

This species is described by Nakai from Hondo, Japan, and based on seven collections (Prov. Sagami, Enosima, *T. Nakai s.n.*, 2 coll., *Yasu-iti Momiyama s.n.*, 2 coll., Hayakawa, *Kiyotaka Hisanti s.n.;* Prov. Izu, Osima, *T. Nakai s.n.;* between Yawatano and Naramoto, *T. Nakai s.n.*). No specimen has been seen by the writer. Nakai mentions: "affinis *S. praecox* et *S. Matsuzakii*, sed a priori foliis sæpe cordato-ovatis grossius serratis, floribus viridulis vel viridi-flavascentibus majoribus, fructibus oblongis vel pyriformibus; et a posteriori caule fruticoso, foliis brevibus cordato-ovatis distinctus est." Again at the end of the description he notes that "this is a coastal plant, easily distinguishable from *S. praecox* by its more vigorous growth, more reddish branchlets, larger shining leaves, longer spikes, and larger paler flowers." From Nakai's original description, the species appears to be particularly close to *S. Matsuzakii* Nakai. As no specimen is available for study, this species is not incorporated in the key.

ARNOLD ARBORETUM, HARVARD UNIVERSITY
JAMAICA PLAIN, MASSACHUSETTS

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 629–632 NOVEMBER, 1943

THE SEPARATION OF ERIGERON FROM CONYZA

ARTHUR CRONQUIST

The preparation of a revision of the North American species of *Erigeron*, in which I am currently engaged, necessitates a careful delimitation of the genus. As is well known, it passes on the one hand into *Aster* and on the other into *Conyza*. In distinguishing it from *Aster*, I have found necessary only minor changes, involving individual species. Its present separation from *Conyza* is much less satisfactory, however, and merits detailed consideration.

The genus *Conyza*, as now commonly treated, differs from *Erigeron* in having no ligules at all on the numerous multiseriate pistillate flowers. This despite the fact that Bentham and Hooker[1] admit that *Conyza* may sometimes have narrow ligules shorter than the styles, and indicate that *C. absinthiaefolia* DC. sometimes has short ligules and sometimes lacks them. Bentham,[2] in a classic paper on *Compositae*, says: "To distinguish, however, *Conyza* and *Erigeron* from *Aster*, we have but little besides the increase in number and reduction in size of the female florets, which in *Erigeron*, although they have still the corollas produced into a ligula, have that ligula always very narrow, and often short; whilst in *Conyza* these corollas are still further reduced to a filiform tube, shorter than the style, toothed or truncate at the top, the ligula remaining undeveloped." A few pages farther on he says of the female florets of *Conyza*, "rarely producing a small scarcely spreading ligula."

The genus *Erigeron* usually has numerous central hermaphroditic flowers, and from few to numerous pistillate flowers with well-developed ligules. In some species the ligules are short or even absent, but the heads seem otherwise unaltered. The tubular pistillate corollas merely lack ligules. Several ordinarily ligulate species have eligulate forms of this type.

In the section *Trimorphaea* (included in *Euerigeron* by Bentham), the most common species of which is *E. acris* L., the corollas of the outer pistillate flowers are very slender and bear short filiform ligules which sometimes do not exceed the pappus. Usually there is an inner series of pistillate flowers with no ligules at all. Here we have an obvious approach toward the *Conyza* type, there being needed to complete the transition merely the disappearance of the already filiform and short ligules, and some decrease in the number of central hermaphroditic flowers. *Trimorphaea* is inextricably bound to *Erigeron*, however, by the obvious evolutionary line of *E. simplex* Greene, *E. uniflorus* L. (*sens. lat.*), and *E. alpinus* L., in which *E. simplex*

[1] Gen. Plant. **2**(1): 283. 1873.
[2] Jour. Linn. Soc. **13**: 335–577. 1873.

is true *Erigeron*, *E. alpinus* is *Trimorphaea*, and *E. uniflorus* is somewhat intermediate.

The next step in the progression toward *Conyza* is furnished by the section *Coenotus*, the most common species of which is *E. canadensis* L. The generic names *Leptilon* Raf. and *Conyzella* Rupr. have sometimes been used for this group by those who were unwilling to include it in *Erigeron* but not bold enough to transfer it to *Conyza*. *Coenotus* differs from *Trimorphaea* in having the central hermaphroditic flowers usually fewer, the pistillate flowers comparatively more numerous, and the ligules reduced so that to casual inspection the heads appear discoid. In the words of Asa Gray,[3] the narrow ligule is "always shorter than its tube, often shorter than the style branches, or even obsolete." Be it noted again that Bentham and Hooker allowed the presence of ligules shorter than the style branches in *Conyza*.

The differences between *Coenotus* and *Trimorphaea* are not great, but the species of the two groups do not seem intimately related. *E. canadensis*, the most nearly bridging species of the section, is scarcely confusable with any species of *Trimorphaea*. Although it is reported to produce a sterile hybrid with *E. acris*,[4] no one familiar with the two species would consider them very closely related.

From *Coenotus* to true *Conyza*, with no ligules at all, is an easy step, as Gray[3] further indicates by the statement, "with the aspect of *Conyza*, and passing into that genus."

Superficially, it seems reasonable to include in *Erigeron* all the species which have any ligule at all, and restrict *Conyza* to the entirely eligulate species. This has been the general practice, despite the fact that Bentham and Hooker admitted to *Conyza* some species with tiny ligules. Unfortunately, the resulting generic segregation is highly artificial. Species which are obviously related to true *Conyza* species, and which have every external appearance of *Conyza*, are found to have tiny ligules, and are thus placed in *Erigeron*. We have *Erigeron microglossus* Blake,[5] the describer of which said, "The species, although of Conyzoid appearance, is technically a true *Erigeron* in the presence of a definite although minute ligule." The ligule is described as being 0.3 mm. long! We have *Conyza mima* Blake,[5] of which Blake said, "The species is named from its great resemblance to *Erigeron subspicatus* Benth., a resemblance so close that except in technical characters of the head the two species can scarcely be distinguished." We have the paired species *Erigeron gnaphalioides* HBK. and *Conyza gnaphalioides* HBK., much confused in herbaria and distinguished chiefly by the fact that the former has tiny ligules. *Conyza Coulteri* Gray is similarly confused with *E. Schiedeanus* Less., for which Gray himself at first mistook it.

[3] Syn. Fl. N. Am. **1**(2): 220. 1884.

[4] Vierhapper, F. Monographie der Alpinen *Erigeron*—Arten Europas und Vorderasiens. Beih. Bot. Centralbl. **19**(2): 385–560. 1906.

[5] Contr. Gray Herb. II. **3**(52): 16–59. 1917.

Descriptions of new tropical species, of Conyzoid aspect, but referred to *Erigeron* because they possess minute ligules, continue to appear intermittently in scientific journals. Long-accepted species of *Conyza* (e.g., *Conyza notobellidiastrum* Griseb.) are transferred to *Erigeron* because the outer florets are found to possess minute ligules. The Gray Herbarium Card Index lists an even dozen South and Central American species of *Conyza* that have been transferred to *Erigeron*. No doubt a thorough inspection of the genus would reveal that other plants still reposing peacefully as species of *Conyza* possess more or less definite ligules. Furthermore, it seems not unlikely that field study of species now known chiefly from herbarium sheets would show some of them to be not entirely constant in the matter of ligules, placing them in company with *C. absinthiaefolia*.

If our taxonomic system is to be merely a series of convenient pigeonholes whereby plants may be catalogued, we may well distinguish *Erigeron* from *Conyza* by the presence of a ligule, even if it be microscopic. We should then dismember the species which may or may not have ligules, placing the ligulate individuals in one genus, and the eligulate individuals in the other. If, however, we hope to arrive at a natural arrangement, we must seek farther for our distinction.

In surveying the numerous species which link true *Erigeron* to true *Conyza*, we find that in only one place is there any suggestion of a real break. That is between *Trimorphaea* and *Coenotus*. Here at least we are not reduced to separating into different genera species which are almost indistinguishable. I therefore propose that the section *Coenotus* be transferred in toto to *Conyza*, and expanded to include all the species of the genus which ordinarily possess ligules.

Conyza and *Erigeron* are redefined as follows:

Conyza: Central hermaphrodite flowers few; pistillate flowers numerous, with filiform corollas; ligules, if present, inconspicuous, shorter than the tubes and scarcely if at all exceeding the pappus.

Erigeron: Central hermaphrodite flowers many, or sometimes rather few; pistillate flowers few to numerous, sometimes with filiform corollas, but then the outer at least with definite ligules equalling or surpassing the pappus.

Even as redefined, the two genera are not sharply distinct, as will be noted from the foregoing characterizations. In America, little or no trouble will be encountered in placing any particular species in the proper genus. In the old world it may sometimes be more difficult, for it is there that the section *Trimorphaea* reaches its greatest development. I believe that the most satisfactory procedure, in any doubtful case, will be to refer the species in question to the genus to which its nearest relatives belong. In some cases this may necessitate considerable study, but the result will be a more nearly natural delimitation of the genera involved. Precisely the same type of situation exists in distinguishing *Erigeron* from *Aster*. It has already in some

cases been met in the fashion here proposed, by referring the species to the genus to which its nearest relatives belong. *Erigeron peregrinus* (Pursh) Greene, for example, is correctly treated by almost all modern American botanists as being an *Erigeron* rather than an *Aster,* because it is closely related to undoubted species of *Erigeron,* although on the basis of technical characters it might better be placed in *Aster.*

Some minor points which may have some bearing may be mentioned. The genus *Conyza* is largely tropical, and according to Bentham (2), "ranges over the warmer regions of Asia, Africa, and America." Further, Bentham says, "*Euerigeron* . . . belongs to the northern hemisphere, and is chiefly mountainous. . . . *Coenotus,* the section which passes into *Conyza,* is now pretty nearly cosmopolitan, and like *Conyza,* overruns tropical as well as temperate regions, the preponderance of local species being African as well as American. . . . The well known *E. canadensis* . . . is almost intermediate between *Coenotus* and *Euerigeron.*" Thus we see that in distribution *Coenotus* is more nearly like true *Conyza* than like true *Erigeron.* The weedy habit of *E. canadensis* is quite in keeping with that of some species of true *Conyza.* Furthermore, the species (*E. canadensis*) which is most nearly intermediate between *Coenotus* and true *Erigeron* is certainly of Conyzoid aspect, and does not seem closely related to any species of undoubted *Erigeron.*

I shall publish formal transfers for only a few American species. The rest I leave to others who may be more conversant than I with the individual species concerned.

Conyza araneosa (Urb.) Cronquist, comb. nov. *E. araneosus* Urb. Symb. Antill. **3**: 404. 1902.

Conyza bonariensis (L.) Cronquist, comb. nov. *E. bonariensis* L. Sp. Pl. **2**: 863. 1753.

Conyza canadensis (L.) Cronquist, comb. nov. *E. canadensis* L. Sp. Pl. **2**: 863. 1753.

Conyza confusa Cronquist, nom. nov. *E. gnaphalioides* HBK. Nov. Gen. **4**: 88. *pl. 331.* 1820. Not *Conyza gnaphalioides* HBK.

Conyza eriophylla (Gray) Cronquist, comb. nov. *E. eriophyllus* Gray, Pl. Wright. **2**: 77. 1853.

Conyza microglossa (Blake) Cronquist, comb. nov. *E. microglossus* Blake Contr. Gray Herb. II. **3**(52): 31. 1917.

Conyza parva Cronquist, nom. nov. *E. pusillus* Nutt. Gen. **2**: 148. 1818. Not *Conyza pusilla* HBK.

Conyza ramosissima Cronquist, nom. nov. *E. divaricatus* Michx. Flor. Bor.-Am. **2**: 123. 1803. Not *Conyza divaricata* Spreng.

Conyza Schiedeana (Less.) Cronquist, comb. nov. *E. Schiedeanus* Less. Linn. **5**: 145. 1830.

Conyza subspathulata Cronquist, nom. nov. *E. spathulatus* Vahl. in West, Bidrag Ste. Croix. 303. 1793. Not *Conyza spathulata* Hornem.

DEPARTMENT OF BOTANY, UNIVERSITY OF MINNESOTA
MINNEAPOLIS, MINNESOTA

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, NO. 6, pp. 633–637 NOVEMBER, 1943

SUPPLEMENTARY NOTES ON THE AMERICAN SPECIES OF ERYTHRINA—II

B. A. KRUKOFF

Through the courtesy of the curators of the botanical institutions mentioned below I was privileged recently to study their collections of *Erythrina*. Many of these collections are not represented by duplicates in American and European herbaria. Extensive collections of *Erythrina* by Drs. Paul C. Standley and Julian A. Steyermark recently made in connection with their work on the flora of Guatemala also became available to me.

Dr. Karl Folkers, Mr. J. Shavel, Jr., and Mr. F. Koniuszy of the Merck Research Laboratory have continued their studies of the alkaloids derived from seeds of various species of *Erythrina* (1, 2, 3) whereas Dr. E. S. Harrar of Duke University has recently undertaken a study of the wood anatomy of species of this genus. In connection with these studies a number of specimens have been received for identification.

The collections examined extend our knowledge of certain species previously known from incomplete material, and extensions of ranges are noted for a number of species. No changes in the nomenclature are necessitated.

The species are arranged in the same order, and the place of deposit of specimens is shown by the same abbreviations as used in my previous papers on *Erythrina* (4, 5). The following new abbreviations are used:

Geor: Georgetown Botanic Garden, British Guiana.
Trin: Trinidad Botanical Garden, Port of Spain.
CR: Museo Nacional de Costa Rica, San Jose.
Cuz: Universidad del Cuzco, Peru.

1. ERYTHRINA GLAUCA Willd.

TRINIDAD: cultivated: *Bot. Gard. Trin. 8353* (Trin). COSTA RICA: Puntarenas: *Brenes 3855* (CR). PANAMA: Canal Zone: *White & White 62* (M). Panama: *Allen 1628* (GH, M). COLOMBIA: Valle del Cauca: *Ramos Nunez s.n.* (*Kr. Herb. 15191*). Huila: *Plata Garcia 15* (Col). VENEZUELA: Carabobo: *L. Williams 12336* (F). Apure: *L. Williams 12961* (F, NY). Federal District: *Tamayo 1281* (F, NY); *Brother Elias 138* (A). Bolivar: *L. Williams 12560* (F, NY, A). ECUADOR: Guayas: *Mille s.n.* (*Kr. Herb. 15350*). PERU: Loreto: *Fernandez s.n.* (*Kr. Herb. 15255*). BRITISH GUIANA: Demerara: *Jenman 3916* (Geor).

Local names: Porotillo (Ecuador); Pisamo (Colombia).

The Brenes' specimen is the first record of the species from the province of Puntarenas, the Williams' specimen—from the State of Apure. The collector states on the label (*Tamayo 1284*): "Las flores son comidas por los pájaros llamados 'arrendajos'. Habiendo leído no se si en la relación del

gobernador Pimentel (15. .) que los Indios del valle de Caracas comían la flor del bucare."

2. ERYTHRINA CRISTA-GALLI L.

TRINIDAD: cultivated: *Bot. Gard. Trin. 12729* (Trin). COSTA RICA: San Jose: cultivated: *J. Valerio 1398* (CR). ARGENTINA: *Santini s.n.* (*Kr. Herb. 15233*). Tucuman: *Meyer s.n.* (*Kr. Herb. 15098*).

3. ERYTHRINA FALCATA Benth.

PERU: Cuzco: *C. Vargas C. 2943* (Cuz). BRAZIL: Minas Geraes: *Mello Barreto 1999* (F). ARGENTINA: Buenos Aires: cultivated: *Thays s.n.* (*Kr. Herb. 15396*). Salta: *Meyer 35390*.

4. ERYTHRINA POEPPIGIANA (Walp.) O. F. Cook.

TRINIDAD: cultivated: *Bot. Gard. Trin. 1332* (Trin), *7574* (Trin), *11947* (Trin), *13325* (Trin). NICARAGUA: Managua: cultivated: *Garnier s.n.* COSTA RICA: Cartago: cultivated: *Jorge Leon 769* (CR). COLOMBIA: Valle del Cauca: *Ramos Nunez s.n.* (*Kr. Herb. 15192*). Boyaca: *Cuatrecasas 9676* (US). Putumayo: *Cuatrecasas 11372* (US). VENEZUELA: Carabobo: *L. Williams 12332* (in part, F). Federal District: *Tamayo 1285* (F), *1309* (NY, US).

The Cuatrecasas' specimens are the first record of the species from Boyaca and Putumayo.

6. ERYTHRINA DOMINGUEZII Hassler.

ARGENTINA: Jujuy: *Fawcett s.n.* (*Kr. Herb. 15394*). Chaco: *A. Schulz s.n.* (*Kr. Herb. 15126*), *s.n.* (*Kr. Herb. 15378*).

The Fawcett specimen is the first record of the species from the province of Jujuy.

7. ERYTHRINA VERNA Vell.

BRAZIL: Maranhão: *Froes 11909*. Bahia: *Froes 12664*.

This is the first record of the species from the States of Maranhão and Bahia.

9. ERYTHRINA SPECIOSA Andr.

BRAZIL: Rio de Janeiro: *Tatto 23* (US).

12. ERYTHRINA EDULIS Triana.

COLOMBIA: Antioquia: *Robledo s.n.* (*Kr. Herb. 15158*). Caldas: *Ramos Nunez s.n.* (*Kr. Herb. 15190*). PERU: Cajamarca: *Stork & Horton 10150* (F). Huanuco: *Stork & Horton 9851* (F). Apurimac: *Stork & Horton 10705* (F).

Local names: Poroton (Ecuador); Pajurro (Peru).

This is the first record of the species from the Department of Cajamarca.

13. ERYTHRINA BREVIFLORA DC.

MEXICO: Michoacan: *Martinez s.n.* (*Kr. Herb. 15346*); *Leavenworth 1914* (M). Morelos: *Martinez s.n.* (*Kr. Herb. 15379*).

14. Erythrina leptorhiza DC.
Mexico: Mexico: *Hinton 15402.*

16. Erythrina montana Rose & Standl.
Mexico: Sinaloa: *Gentry 6259* (GH, NY).
This is the first record of the species from the State of Sinaloa.

18. Erythrina pallida Britton & Rose.
Trinidad: *Bot. Gard. Trin. 2831* (Trin), *10557* (Trin), *10896* (Trin), *11186* (Trin), *13324* (Trin), *13330* (Trin), *13332* (Trin); *Britton 2656* (type coll., Trin); *Britton & Hazen 230* (Trin); *Dean s.n.* (*Kr. Herb. 15183*).

19. Erythrina mitis Jacq.
Venezuela: Carabobo: *L. Williams 12471* (US).

23. Erythrina amazonica Krukoff.
Colombia: Putumayo: *Cuatrecasas 10647* (US), *11212* (US).
This is the first record of the species from Colombia.

25a. Erythrina Corallodendrum var. bicolor Krukoff.
St. Lucia: *Ward s.n.* (*Kr. Herb. 15202*).

26. Erythrina cubensis C. Wright.
Cuba: Pinar del Rio: *Acuña s.n.* (*Kr. Herb. 15361*).

27. Erythrina herbacea L.
U. S.: Texas: *Parks s.n.* (*Kr. Herb. 15257*), *s.n.* (*Kr. Herb. 15258*), *s.n.* (*Kr. Herb. 15299*), *s.n.* (*Kr Herb. 15578*). Florida: *Wilmot s.n.* (*Kr. Herb. 15790*); *Killip 32874* (A). Mexico: Tamaulipas: *Cottam 10564* (*Herb. Univ. Utah*). Oaxaca: *Mexia 9302* (F, M).

28. Erythrina coralloides DC.
Mexico: San Luiz Potosi: *Edwards 682* (M). Hidalgo: *Cottam 10491* (*Herb. Univ. Utah*).

29. Erythrina flabelliformis Kearney.
Mexico: Sonora: *Wiggins 7354* (A); *S. White 3126* (GH).

30. Erythrina lanata Rose.
Mexico: Michoacan: *Leavenworth & Hoogstraal 1399* (M).

32. Erythrina Berteroana Urban.
Guatemala: Quezaltenango: *Steyermark 33665* (F). Retalhuleu: *Standley 87847* (F), *87872* (F), *87883* (F), *88413* (F), *88562* (F), *88704* (F). Suchitepequez: *Rosengarten s.n.* (*Kr. Herb. 15141*). Chiquimula: *Steyermark 30932* (F). Santa Rosa: *Standley 78328* (F). Jutiapa: *Standley 75731* (F), *75799* (F); *Steyermark 30382* (F.) Costa Rica: Guanacaste: *Jorge Leon 961* (CR); *Brenes 12621* (CR), *15507* (CR). Puntarenas: *Brenes 22801* (CR). Alajuela: *Brenes 15012* (CR), *17002* (CR); *Krukoff 3a.* San

Jose: *Skutch 4024* (M). PANAMA: Panama: *Allen 1631* (F). Chiriqui: *Davidson 735* (A).

This is apparently the first record of this common and widespread species from the Departments of Suchitepequez, Chiquimula and Jutiapa.

32a. ERYTHRINA GUATEMALENSIS Krukoff.

GUATEMALA: Suchitepequez: *Rosengarten s.n.* (*Kr. Herb. 15124*).
The species has been hitherto known only from Baja and Alta Verapaz.

33. ERYTHRINA AMERICANA Mill.

U. S.: Alabama: cultivated: *? Parks s.n.* (*Kr. Herb. 15298*). Texas: cultivated: *? Parks s.n.* (*Kr. Herb. 15300*), *? s.n.* (*Kr. Herb. 15301*), *? s.n.* (*Kr. Herb. 15302*). MEXICO: Morelos: *Krukoff 1a.* Oaxaca: *Martinez-Calderon 51.*

34. ERYTHRINA STANDLEYANA Krukoff.

CUBA: Pinar del Rio: *Acuña s.n.* (*Kr. Herb. 15403*).

37. ERYTHRINA RUBRINERVIA H. B. K.

COLOMBIA: Caldas: *Ramos Nunez s.n.* (*Kr. Herb. 15193*). Cundinamarca: *Quintero s.n.* (*Kr. Herb. 15234*).
Local names: Chocho colorado (Colombia).

38. ERYTHRINA MEXICANA Krukoff.

MEXICO: Oaxaca: *Mexia 9234* (F). GUATEMALA: San Marcos: *Giesemann s.n.* (*Kr. Herb. 15129*), *s.n.* (*Kr. Herb. 15365*). Quezaltenango: *Steyermark 33556* (F), *33722* (F). NICARAGUA: Granada: *Grant 870.*

This is the first record of the species from Nicaragua. The Guatemalan specimens were collected at altitudes of 1300–1500 meters. Dr. Steyermark states on the labels of his specimens: "Leaves silvery beneath, olive green above, corolla bright red, calyx dull red."

39. ERYTHRINA LANCEOLATA Standl.

COSTA RICA: Alajuela: *Brenes 5892* (CR), *11576* (CR), *13200* (CR), *13201* (CR), *13461* (CR), *15006* (CR), *18938* (CR), *21812* (CR), *21989* (CR). Cartago: *Lankester s.n.* (*Kr. Herb. 15377*).

41. ERYTHRINA GIBBOSA Cufod.

COSTA RICA: Alajuela: *Krukoff 2a; Brenes 4034* (CR), *1113* (CR), *1866* (CR), *5755* (CR), *9364* (CR), *13202* (CR), *20625* (F). Cartago: *Krukoff 5a.* PANAMA: Bocas del Toro: *Woodson et al. 1930* (A); *von Wedel 578* (M), *1196* (M). Chiriqui: *Woodson et al. 913* (A). Cocle: *Allen 110* (A).
Local names: Poro de montana (Costa Rica).

On my recent trip to Costa Rica I became acquainted with the species in the field. It is a very spiny small tree, usually 20–25 ft. high and is common along streams on elevations above 1000 meters, at least in the region of Turrialba (Cartago) and in the region of Buena Vista (Alajuela). At the time of my visit to Costa Rica (August) the majority of trees were in flower and a few had immature fruits. Seeds are uniformly scarlet. The species has been hitherto known in Costa Rica only from the provinces of Alajuela, San Jose and Limon.

42. ERYTHRINA PANAMENSIS Standl.

PANAMA: Bocas del Toro: *von Wedel 1766* (M). Canal Zone: *Marjorie Brown 16* (F). Darien: *Terry 1413* (A, F, M).

43. ERYTHRINA COSTARICENSIS M. Micheli.

COSTA RICA: Guanacaste: *Brenes 15636* (CR). Alajuela: *Krukoff 1a.* Cartago: *Jorge Leon 558* (CR), *768* (CR); *Krukoff 6a, 7a, 8a.*

This large forest tree, often up to 80 ft. high, is common along streams on elevations below 1000 meters at least in the region of Buena Vista (Alajuela).

45. ERYTHRINA MACROPHYLLA DC.

GUATEMALA: Quezaltenango: *Standley 87066* (F).

Standley notes on the label: "Rocky open hillside; alt. 1200–1400 meters; small tree, common; flowers bright red."

50. ERYTHRINA VELUTINA Willd.

TRINIDAD: cultivated: *Bot. Gard. Trin. 10042* (Trin). VENEZUELA: Carabobo: *L. Williams 12332* (in part, F).

THE NEW YORK BOTANICAL GARDEN
NEW YORK

Literature Cited

1. **Folkers, K., J. Shavel, Jr. & F. Koniuszy.** *Erythrina* alkaloids. X. Isolation and characterization of Erysonine and other liberated alkaloids. Jour. Am. Chem. Soc. **63**: 1544–1549. 1941.
2. **Folkers, K. & J. Shavel, Jr.** *Erythrina* alkaloids. XII. Chromatographic analyses of Erysodine, Erysovine and "Erysoeine" and technique for preparative isolation. Jour. Am. Chem. Soc. **64**: 1892–1896. 1942.
3. **Folkers, K., F. Koniuszy & J. Shavel, Jr.** *Erythrina* alkaloids. XIII. Studies on the constitution of Erythraline, Erythramine, and Erythratine. Jour. Am. Chem. Soc. **64**: 2146–2151. 1942.
4. **Krukoff, B. A.** The American species of *Erythrina*. Brittonia **3**: 205–337. 1939.
5. ————. Supplementary notes on the American species of *Erythrina*. I. Am. Jour. Bot. **28**: 683–691. 1941.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 70, No. 6, pp. 638–650 NOVEMBER, 1943

THE NORTH AMERICAN VARIATIONS OF DISTICHLIS SPICATA

ALAN A. BEETLE

The genus *Distichlis* of the Gramineae (tribe Festuceae) presents an unusual problem among the grass genera of North America because of its dioeciousness. The members are primarily grasses of alkaline situations, hence the common name "salt grass." This author recognizes three species in North America, *Distichlis spicata* (L.) Greene (a complex consisting of several well marked geographical varieties), *D. texana* (Vasey) Scribn., and *D. palmeri* (Vasey) Fassett. These last two are so easily distinguished by their large size and long spikelets as to need no further discussion here. Outside of North America the genus is represented by *D. distichophylla* (Labill.) Fassett in the south Australian area, in South America by *Distichlis spicata* where again it seems to be broken up into well-defined geographical varieties, and by *D. scoparia* (Kunth) Arech.

Rafinesque (1819) first proposed *Distichlis*, separating it from *Uniola* and *Festuca* and including *D. maritima* (*D. spicata*) and *D. nodosa* (also *D. spicata*). For nearly a century most botanists were content to call all the North American material of this complex one species, whether found on the Atlantic coast, on the Pacific coast, or inland in the dry basins of the West. That the species *Uniola stricta* of Torrey (1824) was but a variety of *D. spicata* was reasoned many times over a long period by Gray (1871 as *Brizopyrum*), Thurber (1880), and Scribner (1894). Recently there has been a tendency to find specific differences between *D. stricta* and *D. spicata*; see Rydberg (1909), Fassett (1925) and Hitchcock (1935). Most of these studies were carried on with reference to a limited amount of California material. It was the additional evidence from this polymorphic group which made the present study seem worth while.

Fassett (1925) has built up the best case for the maintenance of *Distichlis stricta* (Torr.) Rydb. as a species. In his treatment he confines *D. spicata* to the east coast of North America and the Puget Sound region while the rest of the North American material, whether inland or on the California coast, is called *D. stricta*. His separation is as follows:

D. spicata	*D. stricta*
compact panicles	more open panicles
10–20 spikelets	16–24 spikelets
♀ spikelets slightly firmer than the staminate	♀ spikelets firm and coriaceous, the staminate papery
spikelets 4–9-, rarely 12-flowered	spikelets 6- to 18-flowered
lemmas 4.5–7.8 mm. long (except in a few plants)	lemmas 3.2–5 mm. in length

D. spicata	*D. stricta*
grain 2 mm. long, ovoid, and not much narrowed below the two beak-like styles	grain 2.5–5 mm. long, narrowed to an attenuate style, which is sometimes split, but hardly into two distinct styles
leaves smooth-edged and blunt or oblique at the tip	leaves sharp-pointed and serrate at the tip

That *Distichlis dentata* Rydb., "described as differing from *D. spicata* and *D. stricta* in having broader leaves, spikelets, glumes and paleas and dentate keels on the paleas," differs "only in degree" was concluded by Fassett, and has recently been corroborated by Reeder (1943). This conclusion is again reached here but it is further maintained that the differences between *D. spicata* and *D. stricta* are not sufficiently constant to treat the entities as more than geographical varieties.

There are no more compact spikes (either staminate of pistillate) than those found in the material from coastal California; on this character as well as leaf serration and tip, and achene measurement the material should fall with *D. spicata*, but, as pointed out by Fassett (1925), the characters of the palea and lemma are closer to those of *D. stricta*. The number of spikelets in material from California has been found to vary from 3 to 60 in pistillate plants and from 3 to 20 in staminate plants. The great variation in texture of both the palea and the lemma, usually correlated with the width of the base of the lemma, is recognized, but no pattern of discontinuity has been discovered. In general the plants which Hitchcock has maintained represent *D. stricta* as opposed to *D. dentata* have narrow spikelets with less firm lemmas and paleas and lack the conspicuously dentate palea wings. There is certainly no dividing line. Some specimens from California are no different in texture from those of the Atlantic coast. The number of florets in a spikelet in California material has been counted from 3 to 14 in pistillate plants and from 3 to 20 in staminate plants. The variation in both shape and size measurements of the grains is very confusing. Some of the seeds have a slender attenuate tip while others have an abruptly truncate tip, and every length between 1.5 and 3.5 mm. has been found in apparently fully mature material from western North America. As a result of the foregoing it is concluded that *D. stricta* is not specifically distinct from *D. spicata*.

In reaching this decision it is not sufficient to study only the North American material. There are thirteen independent names (*D. ammobia, araucana, hirta, humilis, laxiflora, marginata, mendocina, misera, prostrata, tenuifolia, thalassica, viridis, volckmanni*) for South American material, which, in light of the heavy conspecificity between the two continents, have a definite bearing on the problem. That other botanists who have dealt with this South American material consider *D. spicata* a single polymorphic species composed of many geographical varieties is indicated by the combinations *D. spicata* var. *humilis* (Phil.) O. Kuntze, var. *marginata* (Phil.) O.

Kuntze., var. *thalassica* (H. B. K.) Ktze., and *D. spicata* var. *mendocina* Hack. Although these varieties are considered to belong to the same species as the North American varieties, they have marked differences, e.g., culm pubescence, and as yet it has not been determined with certainty that any of the varieties occur on both sides of the equator.

Actually it is not enough merely to decide taxonomically that all the strains of a complex comprise a given species. Often names for the entities in subspecific categories are very important. *Distichlis* is one of the few perennial grasses of prostrate habit, spreading by rhizomes (or rarely by stolons) which is adapted to alkaline soils. In the west where large areas are alkaline, covers for air fields and playgrounds are important but difficult to establish. Although *Distichlis* will probably never be highly recommended for forage it seems that some of the strains are much more palatable if not more nutritious than others. An analysis of the various California types seems therefore well justified from a utilitarian standpoint.

Observations in the field tend to indicate that male and female plants occur with approximate frequency throughout the whole range, although often only one or the other is present in a limited area because of vegetative propagation. Although pollen is freely produced and pistillate plants flower abundantly, mature seed is seldom set probably because of (a) the separation into male and female colonies, (b) the extreme xerophytic nature of the habitat which often does not allow sufficient time for full development. Of 332 North American collections of the *Distichlis spicata* complex available for study, which may be taken to comprise a random sampling, 143 were pistillate only, 22 had both pistillate and staminate plants, and 167 were staminate only. As noted by Reeder (1943) there is a noticeable predominance of staminate plants in the *D. stricta* group. Where plants are only vegetative no way has been discovered to determine whether they are male or female, but it is usually possible to determine to what variety they belong on vegetative characters. Even the staminate and pistillate spikes, as mentioned by Hitchcock (1935), are very similar, usually differing to a marked degree only in the palea.

Stebbins and Love (1941) reported 2n = 40 for *Distichlis*, the only chromosome number reported for California material. Holm (1891) was able to recognize as distinct North American entities, based on anatomical evidence, the following: *D. maritima* (Atlantic coast), *D. maritima* var. *stricta* (Nebraska), *D. maritima* var. *laxa* (Utah), *D. thalassica* H. & K. (Lower California), *D. prostrata* (Mexico). This author is unable to appraise the significance of the rather incomplete data.

California material of *Distichlis* often displays insect galls caused by the fly, *Chlorops graminea* Coq.

Since much of the confusion in determining plants in the past has been over staminate and pistillate plants it was decided here to treat each separately. The plants were first separated arbitrarily into males and females and then separated into units on the basis of the female plants only. It was then considered significant that the male plants from the same region had the same vegetative characters.

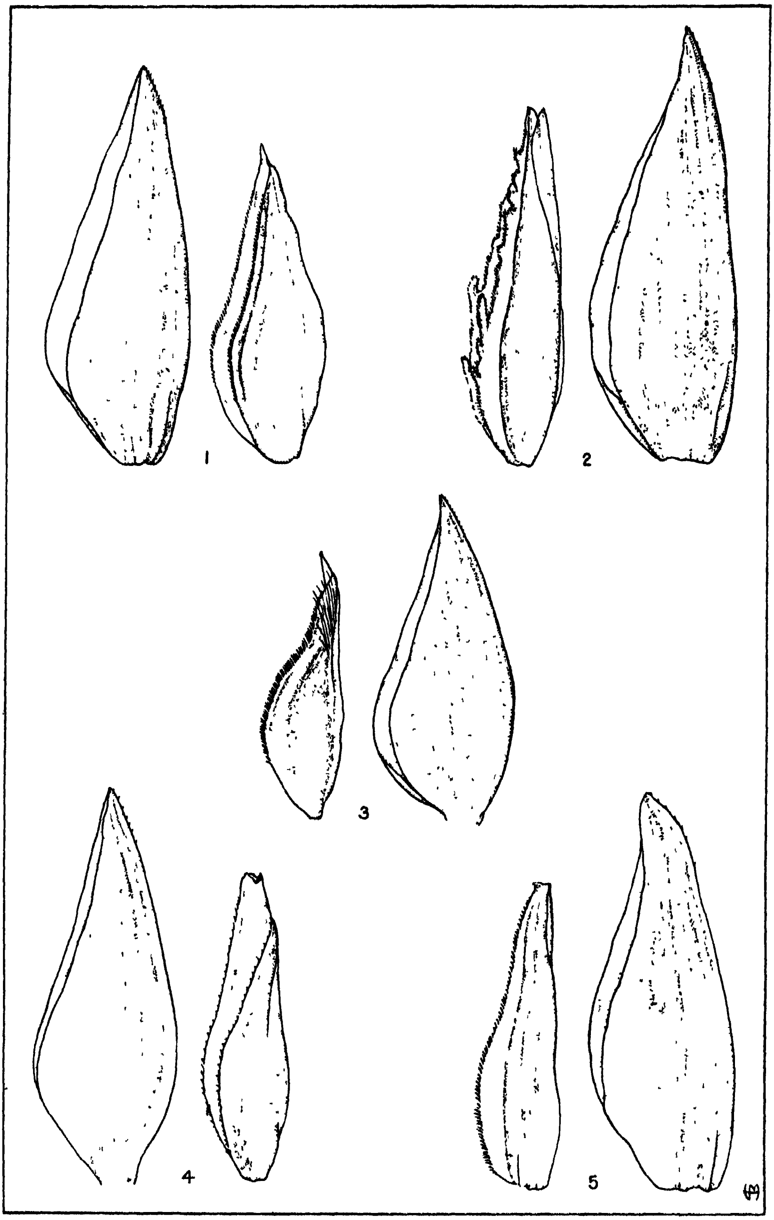
In the preparation of this paper material from the following herbaria has been examined: Agronomy Division Grass Herbarium (AG), College of Agriculture, Univ. of California, Davis; Botany Department, University of California (UC), Berkeley; Dudley Herbarium (D), Stanford University; California Academy of Sciences. In the interest of brevity the source of the specimens except types will not be further specified.

DISTICHLIS RAFINESQUE

Dioecious perennials; culms wiry, upright from strong, creeping, or deeply-running rhizomes; ligule short and evenly serrate; leaf-blades noticeably, often stiffly 2-ranked, flat or somewhat involute; staminate spike exceeding the blades, the blades usually equalling or exceeding the pistillate; spikelets in open or dense spikes, few to many flowered; glumes unequal, broad, 3–7 nerved; lemmas closely to loosely inbricate, 9–11 nerved, coriaceous; palea usually a little shorter than the lemma, two keeled, serrate on the keels, often with a few long hairs on the back, the nerves sometimes excurrent; caryopsis brown; stamens 3.

Plants pistillate
- Spikes congested, the short pedicels hidden, of uniformly 5–9 flowered spikelets
  - Spikes narrow, culms strictly erect, never stoloniferous, often 3–6 dm. long
    - Outer glume 3 mm. long, second glume 4 mm. long; lemma ca. 6–10 nerved — 1. *D. spicata*
    - Outer glume 2.5 mm. long, second glume 3 mm. long; lemma ca. 12–14 nerved — 2. *D. spicata* var. *borealis*
  - Spikes oval, culms usually prostrate, often stoloniferous, up to 3 dm. long — 3. *D. spicata* var. *stolonifera*
- Spikes of approximate but rarely congested spikelets, the pedicels readily visible, the number of florets very variable (3–14)
  - Leaves divaricate, culms and leaves rigid — 4. *D. spicata* var. *divaricata*
  - Leaves mostly ascending, culms and leaves lax
    - Blades long (1–2 dm.), equally spaced on the culm, often equalling or exceeding the spikes; spikelets 4–6 mm. broad — 5. *D. spicata* var *stricta*
    - Blades short, seldom 1 dm. long, usually crowded at the base, and exceeded by the spikes, spikelets 2–4 mm. broad
      - Palea broadly winged at base, usually hairy on the back — 6. *D. spicata* var. *nana*
      - Palea narrowly winged at base, glabrous on the back — 7. *D. spicata* var. *mexicana*

Plants staminate (a rudimentary pistil often present)
- Spikes congested, of uniformly 5–9-flowered spikelets, the blades usually equalling the spike



FIGS. 1–5. Sample pistillate lemmas and paleas of the *Distichlis spicata* complex. FIG. 1. *D. spicata* var. *borealis*, drawn from Vancouver Island material. FIG. 2. *D. spicata* var. *stricta*, drawn from *Sandberg & Leiberg 468*, the co-type of *D. dentata*. FIG. 3. *D. spicata* var. *nana*, drawn from the type. FIG. 4 *D. spicata* var. *stolonifera*, drawn from the type. FIG. 5. *D. spicata* var. *mexicana*, drawn from the type.

Culms strictly erect, spikelets pale green or slightly purplish
Florets mostly 5–6 per spikelet; leaves 1–2.5 cm. apart on culm usually 1. *D. spicata*
Florets mostly 7–10 per spikelet; leaves 1.5–6 cm. apart on culm 2. *D. spicata* var. *borealis*
Culms somewhat prostrate, often stoloniferous; spikelets strongly purplish 3. *D. spicata* var. *stolonifera*
Spikes approximate but rarely congested; the blades not usually equalling the spike
Leaves divaricate, culms and leaves rigid 4. *D. spicata* var. *divaricata*
Leaves mostly ascending, culms and leaves lax
Blades long (1–2 dm.); spikelets 4–6 mm. broad 5. *D. spicata*. var. *stricta*
Blades short, seldom up to 1 dm. long; spikelets 3–4 mm. broad
First glume 2 mm. long, second glume 3 mm. long; anthers 2 mm. long 6. *D. spicata* var. *nana*
First glume 3 mm. long, second glume 4 mm. long; anthers 3 mm. long 7. *D. spicata* var. *mexicana*

1. Distichlis spicata (L.) Greene.

Culms 1–6 dm. tall, slender, erect; blades erect up to 1.5 dm. long, 1–2.5 cm. apart on the culm; equaling or exceeding the pistillate spikes and rarely exceeded by the staminate spikes; pistillate spikes pale green, 1–6 cm. long, of 8–36 congested spikelets, these spikelets 5–9 flowered, up to but not exceeding 1 cm. long, 4 mm. broad, the first glume 3 mm., second glume 4 mm. long, the lemmas 6–10 nerved, 3.5–4 mm. long, closely imbricate, the palea 2-keeled, the keels minutely, evenly serrate, the 4 nerves often excurrent; caryopsis ca. 2 mm. long, somewhat truncate at the tip.

Staminate spike pale green, 1–6 cm. long, of 6–30 congested spikelets; the spikelets 7–10 flowered, ca. 1 cm. long, 4 mm. broad, the first glume up to 3 mm. long, the second glume up to 4 mm. long, the lemmas 6–10 nerved, 3 mm. long, the palea 2 keeled but otherwise nerveless, ca. 3 mm. long; anthers ca. 2–3 mm. long.

Type locality: Atlantic Coast of North America.

Range: Coastal salt marshes, Prince Edward Island to Florida; West Indies; Louisiana; Texas.

Since any of the collections made in this range may be considered representative of typical *Distichlis spicata* (L.) Greene, no specimens will be cited.

2. D. spicata var. **borealis** (Presl) Beetle, comb. nov.

Brizopyrum boreale Presl, Rel. Haenk. **1**: 280. 1830.

Culms 2–4 dm. tall, erect; blades erect, exceeding the pistillate spikes and rarely exceeded by the staminate; pistillate spikes pale green or slightly purplish, 2–6 cm. long, of 10–60 congested spikelets; the spikelets ca. 1 cm. long, 4 mm. broad, 5–9 flowered, the florets closely imbricate, the first glume 2.5 mm. long, second glume 3 mm. long, the lemmas 12–14 nerved, 4.5 mm. long; the palea 3.5 mm. long, evenly serrate on the keels, nerveless, the caryopsis ca. 2 mm. long, somewhat truncate at the tip. (Figs. 1, 8.)

Staminate spikes pale green or slightly purplish, 2.5–5 cm. long, of 6–30 congested spikelets, the spikelets up to ca. 1 cm. long, 4 mm. broad, 5–0 flowered, the florets closely imbricate, the first glume ca. 3 mm. long, second glume 3.5 mm. long, the lemmas 4.5 mm. long, 8–12 nerved, usually not

scabrous on the back, the palea 3.5–4 mm. long, serrate on the keels, nerveless; anthers ca. 3 mm. long.

Type locality: Nootka Sound, Vancouver Island, *Haenke.*

Female: British Columbia, Crescent Beach, *Eastham 9920*, Cadboro Bay, *Pineo* in 1894. Washington, Clallam Co., *Elmer 1667;* San Juan Co., *Roush* in 1919; Twin Island, *Berg 32*, King Co., *Thompson 5232*. Male: British Columbia, Sooke Harbor, *Pineo* in 1898. Washington, Whatcom Co., Kitsap Co., *Otis 1635.*

Distichlis spicata var. *borealis* is in many respects intermediate between the typical material on the east coast of North America and *D. spicata* var. *stolonifera.* The Puget Sound material has the tall erect habit of typical *D. spicata* as well as the narrow spikes but in the purplish color of the spikes and many of the technical measurements suggests the var. *stolonifera.*

3. D. SPICATA var. **stolonifera** Beetle, var. nov.

Culms up to 3 dm. tall, often prostrate, with a strong tendency to produce stolons; blades erect, mostly 1–2 dm. long, the upper exceeding the pistillate spike and usually equalling the staminate; pistillate spike green or often strongly purplish, oval, club-shaped, 1.5–5 cm. long, often 2 cm. thick, of 8–35 congested spikelets, the spikelets 5–9 flowered, closely imbricate, ca. 1 cm. long or rarely longer, 4 mm. broad, the outer glumes 2.5 mm. long, second glume 3.5 mm. long, the lemmas 5 mm. long, faintly nerved, the palea 2-keeled, broadly winged below, with very hyaline margins, serrate on the keels above but smooth at the base, caryopsis ca. 2 mm. long, broadest at the base, slightly truncate at the tip. (Figs. 4, 12.)

Staminate spikes green or often strongly purplish, 1.5–5.5 cm. long, of 6–20 congested spikelets often interrupted below, the spikelets 7–10 flowered, ca. 1 cm. long, 4 mm. broad, the first glume ca. 3 mm. long, the second glume ca. 3.5 mm. long, the lemmas 3.5 mm. long, faintly nerved and weakly scabrous, the palea subequal with or slightly longer than the lemma, the keels minutely, evenly serrate above, the margins hyaline, nerveless, anthers 2.5 mm. long. (Fig. 7.)

Culmi saepe prostratae, saepe stoloniferae; spicae feminae viride aut saepe forte purpurascentes, ovatae, cum 8–35 congestae spiculae; spiculae cum 5–9 florae. Spicae masculinae viridae aut saepe forte purpurascentes, cum 6–20 congestae spiculae; lemmae circa 3.5 mm. longae; paleae subaequalae, bicarinatae.

Type locality: near Ferndale, Humboldt Co., California (pistillate), July 30, 1899. *J. B. Davy & W. C. Blasdale 6202* (UC). Co-type: Arcata, Humboldt Co., California (staminate), June 17, 1899. *J. B. Davy & W. C. Blasdale 5604* (UC).

Female: California, Humboldt Co., Eureka, *Yates 5859;* Marin Co., Point Reyes, *Davy 6736;* Contra Costa Co., Point Richmond, *Beetle 1752;* Alameda Co., West Berkeley, *Davy 856;* near San Francisco, *Bolander 1527;* San Mateo Co., *Beetle 1888;* Santa Cruz Co., Santa Cruz, *Thompson* in 1903; Monterey Co., Monterey, *Elmer 4042;* Orange Co., s. of Laguna Beach, *Beetle 3099;* San Diego Co., Coronado, *Chandler 5164.*

Male: Oregon, Netarts, *Thompson 3150.* California, California, Humboldt Co., Eureka, *Stebbins & Church 3104;* Mendocino Co., Fort Bragg, *Davy & Blasdale 6125;* Marin Co., *Davy 4039;* Contra Costa Co., *Wiesendanger 1534;* Alameda Co., Hayward, *Nixon* in *1915;* San Francisco, *Bolander 1527;* Santa Clara Co., near Alviso, *Dudley* in 1903; Monterey Co., Del Monte, *Elmer 4042;* Santa Barbara Co., Santa Barbara, *Elmer*

3902; Los Angeles Co., Pebble Beach, *Fosberg S4475*; Orange Co., s. of Laguna Beach, *Beetle 3099*.

The most characteristic and strongly stoloniferous material of this variety is found at certain points along the coast, namely at Humboldt Bay, San Francisco Bay, Monterey Bay and Orange County. Material from other points along the coast is less stoloniferous but agrees in technical points. In the coast hills and inland marshes there is a considerable amount of intergradation, although most of this material is nearer to var. *stricta*.

4. D. SPICATA var. **stricta** (Gray) Beetle, comb. nov.

Brizopyrum spicatum var. *strictum* A. Gray; S. Wats., in King, Geol. Expl. 40th Par. 5: 385. 1871. (Based on *Uniola stricta* Torr.)

Culms 1–3.5 dm. tall, erect or rarely decumbent, the blades up to 2 dm. long, the upper equalling or exceeding the pistillate spikes but exceeded by the staminate; pistillate spike green drying straw brown, 2–7 cm. long; of 5–40 approximate spikelets, the spikelets 0.5–2 cm. long, 5–20-flowered, 4–7 mm. broad, the mature florets often strongly reflexed, usually not closely imbricate, the first glume 2–3 mm. long, the second 3–4 mm. long, the lemma 3.5–6 mm. long, firm, with a broad hyaline margin, the palea 3–5 mm. long, the keels conspicuously serrate to the base, often dentate, narrow or winged at the base, occasionally with a few long hairs on the back, the caryopsis 2–5 mm. long, sometimes slenderly tapered to a single beak, sometimes truncate with a double beak. (Figs. 2, 11, 13.)

Staminate spike green or rarely purplish, drying straw brown, 2–5 cm. long, of 5–25 approximate spikelets, the spikelets 0.5–2 cm. long, 5–20-flowered, 4–7 mm. broad, closely imbricate, the first glume 2–3 mm. long, the second 3–4 mm. long, the lemmas 5–6 mm. long, firm, equaled by the palea, the palea 5–6 mm. long, the keels conspicuously serrate to the base, infrequently dentate, rarely broadly winged, usually with at least one prominent marginal vein, the anthers 3–4 mm. long. (Fig. 6.)

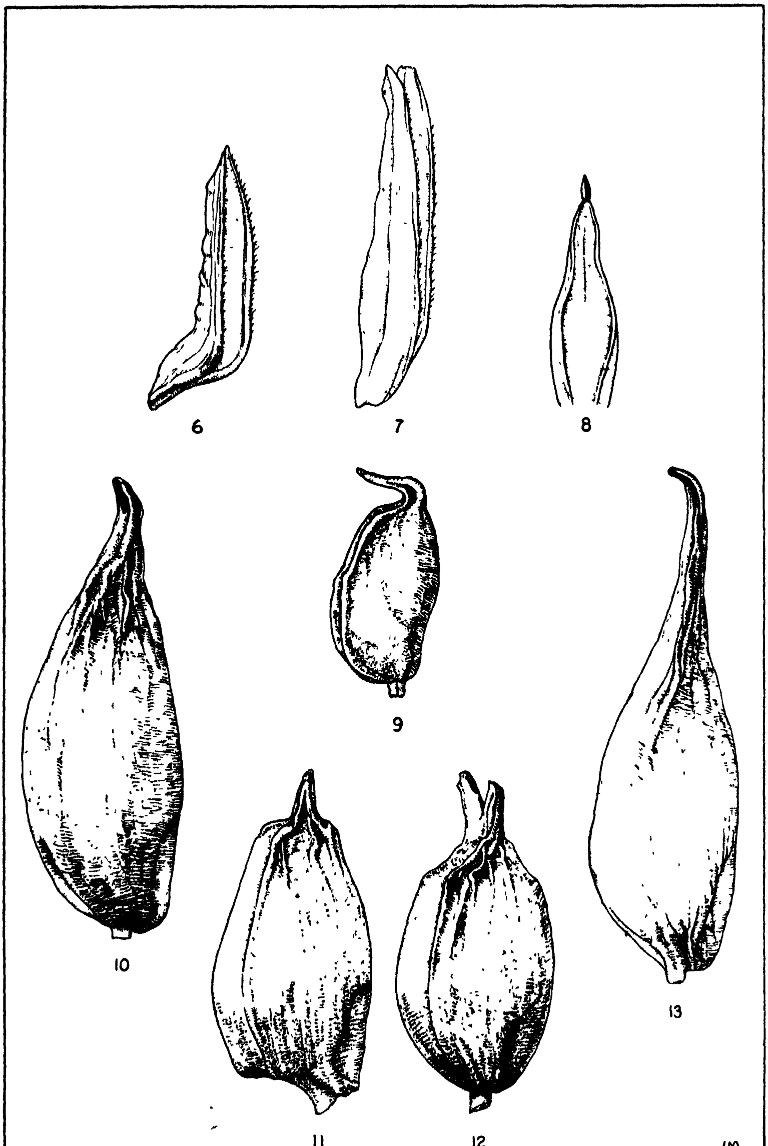
Type locality: Canadian River, Oklahoma.

Range: Alkaline situations; Saskatchewan south through N. D., S. D., Kansas, Nebraska, Oklahoma, and Texas and west to the Pacific Coast.

D. spicata var. *stricta* has the widest range of any of the varieties. In various parts of its range it approaches in certain characters all the other varieties and even the typical material from the eastern seaboard. The amazing variations in the caryopsis suggests the following hypothesis. *Distichlis* might be called an evergreen grass. It needs only sufficient warmth and moisture to start new growth. Yet its xerophytic habitat seldom gives it a prolonged period of growth for most of the time it is either too cold or too dry. Some achenes are produced in the cold wet winters and some in the hot, dry summers and many are caught in a partially mature condition when growth ceases. It is very possible that here is a case in which some of the reproductive structures are of less importance than the vegetative.

In California the range of the species is disrupted by the Sierra Nevada and Tehachapi Mountains.

Modoc County, *Manning 423*, Siskiyou Co., *Butler 1844*; Lassen Co., *Beetle 2807*; Glenn Co., *Davy* in 1898; Sierra Co., *Lemmon* in 1874; Colusa Co., *Beetle 3270*; Yolo Co., *Raynor* in 1939; Alameda Co., *Yates 5503*; Mono Co., *Rose 35416*; Merced Co.,



FIGS. 6–8. Staminate paleas. FIG. 6. *D. spicata* var. *stricta*, drawn from Santa Barbara Co., Calif., material. FIG. 7. *D. spicata* var. *stolonifera*, drawn from Alameda Co., Calif., material. FIGS. 9–13. Sample grains of the *D. spicata* complex. FIG. 9. *D. spicata* var. *nana*, drawn from Merced Co., Calif., material. FIG. 10. *D. spicata* var. *divaricata*, drawn from Imperial Co., Calif., material. FIG. 11. *D. spicata* var. *stricta*, drawn from *Sandberg & Leiberg 468*, the co-type of *D. dentata*. FIG. 12. *D. spicata* var. *stolonifera*, drawn from San Mateo Co., Calif., material. FIG. 13. *D. spicata* var. *stricta*, drawn from Nebraska material.

Howell 2046; Kings Co., *Beetle 2981*; Tulare Co., *Palmer 2754*; Inyo Co., *Beetle 3669*; Kern Co., *Davy 1842*; San Luis Obispo Co., *Johannsen 1190*; Ventura Co., *Simontacchi 112*; San Bernardino Co., *Beetle 3204*; Orange Co., *Wolf 3785*; Riverside Co., *Koethen* in 1897; San Diego Co., *Chandler 5227*.

5. D. SPICATA (L.) Greene var. **nana** Beetle, var. nov.

Culms erect, very slender, 1–4 dm. tall, the blades up to 6 dm. long, rarely longer, exceeded by both the staminate and pistillate spikes, often crowded at the base, the pistillate spikes green or purplish, drying brown, 1–4 cm. long, of 3–12 approximate spikelets, the spikelets 0.5–2 cm. long, 3–18-flowered, 3–4 mm. broad, closely imbricate, the first glume ca. 3 mm. long, the second glume 3.5 mm. long, the lemmas ca. 3.5 mm. long, very broad at the base, 9-nerved, the palea subequal, very strongly ciliate on the keels, abruptly winged below, with a single prominent marginal nerve, the caryopsis ca. 2 mm. long, abruptly truncate at the apex, the apex often bent. (Figs. 3, 9.)

Staminate spike green or purplish, drying brown, 1–4 cm. long, of 3–12 approximate spikelets, the spikelets 0.5–2 cm. long, 3–16-flowered, 3–4 mm. broad, closely imbricate, the glumes ca. 3 mm. long, the lemma ca. 3.5 mm. long, broad at the base, 9-nerved, the palea subequal, evenly ciliate on the narrow keels, anthers ca. 2 mm. long.

Culmi erectae, summe graciles, 1–4 dm. alti, laminae generalis usque ad 6 dm. longae, saepe basi confluenti, spicae feminae viride aut purpurascentes, cum 3–12 propinquae spiculae; spiculae propinquemente imbricatae, cum 3–18 florae, lemmae circa 3.5 mm. longae; paleae subaequalae, bicarinatae. Spicae masculinae viridae aut purpurascentes, cum 3–12 propinquae spiculae, spiculae cum 3–16 florae.

Type locality: California, Tulare County, Whitaker Forest, June 28, 1928, P. B. Kennedy (AG). Co-type: California, Kern County, near Bakersfield, 1896, *J. B. Davy 1841* (UC).

Female: California, Tehama Co., w. of Red Bluff, *Beetle 3285*; Kern Co., McKittrick, *Yates 6511*; Tulare Co., Whitaker Forest, *Kennedy* in 1928; Santa Barbara Co., w. of Cuyama Ranch, *Beetle 3031*; Merced Co., e. of San Joaquin R., *Stebbins 2798*; Stanislaus Co., w. of Modesto, *Beetle 2941*; Monterey Co., s.w. of Bradley, *Grahm 376*; San Diego Co., Escondido, *Meyer 151*; Lassen Co., Amedee, *Davy* in 1897.

Male: California, Stanislaus Co., *Sharsmith 3777*; Kings Co., s. of Armona, *Beetle 2967*; Kern Co., near Delano, *Davy 2146*; Tulare Co., Visalia, *Dudley* in 1900; Alameda Co., n.w. of Halfway House, *G. L. Stebbins 2736*; Fresno Co., Huron, *Eastwood* in 1893.

This variety is often reported collected on soils which seem to be hardly if at all alkaline. It has the finest leaves and would seem to be the most palatable for stock.

6. D. SPICATA (L.) Greene var. **divaricata** Beetle, var. nov.

Culms 1–4 dm. tall, very stiffly erect, the blades rarely exceeding 5 cm. in length, rigid, divaricate, exceeded by both the staminate and pistillate spikes, the pistillate spike green or purplish quickly turning brown, 2–6 cm. long of 6–20 approximate spikelets, the spikelets 0.5–1.5 cm. long, 5–12-flowered, 3–6 mm. broad, the first glume 3 mm. long, the second glume 3–3.5 mm. long, the lemma ca. 4 mm. long, broad below, without prominent nerves, the palea ca. 3.5 mm. long, often dentate, conspicuously serrate on the keels,

usually without prominent nerves, the caryopsis 2–3 mm. long, plump, usually somewhat tapered to a single apex. (Fig. 10.)

The staminate spike green or purplish quickly turning brown, 2–6 cm. long, of 6–15 approximate spikelets, the spikelets 0.5–1.5 cm. long, 5–12-flowered, 3–6 mm. broad, the first glume ca. 3 mm. long, the second glume nearly subequal, the lemmas ca. 4 mm. long, broad below, without prominent nerves, the palea subequal, very narrow, nerveless, the anthers 2–2.5 mm. long.

Culmi 1–4 dm. alti, summe erecti rigide, laminae generalis usque ad 5 cm. longae, rigidae, divaricatae; spicae feminae viride aut purpurascentes, cum 6–20 propinquae spiculae, spiculae cum 5–12 florae, lemmae sinae prominentae nervae; paleae saepe dentatae; gramen pinquis. Spicae masculinae viridae aut purpurascentes, cum 6–15 propinquae spiculae, spiculae cum 5–12 florae, sine prominentae nervae; paleae subaequalae, summe angustae, sine nervae.

Type locality: California, Riverside Co., Salton, *J. B. Davy* in 1902 (UC). Co-type, California, Imperial Co., Salton Sink, March 17, 1917, *E. A. McGregor 779* (Dudl).

Female: California, Kern Co., near Rosamond, *Davy 2944;* Mexico, western Sonora, 1898, *W. W. Price;* Sonora, *Wiggins 8587,* Baja Calif., *Wiggins & Gillespie 4171.*

Male: California, Mojave, *M. E. Jones* in 1917, Death Valley, *Grinnell* in 1917. Mexico, Baja Calif., n. of Ensenada, *Wiggins & Gillespie 3920.*

7. DISTICHLIS SPICATA (L.) Greene var. **mexicana** Beetle, var. nov.

Culms 1–3 dm. tall, erect, rather slender; blades erect, up to 1 dm. long, the upper about equalling the pistillate spikes and exceeded by the staminate, the pistillate spike green, 3–5 cm. long, of 6–16 approximate spikelets, the spikelets 0.5–1.5 cm. long, 3–4 mm. broad, the upper often curved, of 3–12 florets, the first glume ca. 3 mm. long, the second 3.5 mm. long, the lemma prominently 9-nerved, very broad below with a hyaline margin, ca. 5 mm. long, the palea subequal, serrate on the often dentate keel, with a single prominent marginal vein, the caryopsis plump at the base, gradually tapered to the apex. (Fig. 5.)

Staminate spike green or purplish, 1.5–8 cm. long, of 6–15 approximate spikelets, the spikelets 0.5–1.5 cm. long, 3–4 mm. broad, the upper often curved, of 3–12 florets, the first glume ca. 2 mm. long, the second 3–3.5 mm. long, the lemmas prominently 9-nerved, broad below, with a hyaline margin, the palea subequal, serrate on the keels, narrow above and slightly broadened below, the anthers 3–4 mm. long.

Culmi 1–3 dm. alti, erecti, aliquanti graciles; laminae erectae, usque ad 1 dm. longae; spicae feminae cum 6–16 propinquae spiculae, spiculae superioribus saepe flexi, cum 3–12 florae, lemmae et paleae subaequalae. Spicae masculinae, viridae aut purpurascentes, longae, cum 6–15 propinque spiculae, spiculae superioribus saepe flexi, cum 3–12 florae.

Type locality: Mexico, city of Durango, 1896, *E. Palmer 388* (UC) (pistillate). Co-type: Mexico, city of Durango, *E. Palmer 182* (UC) (staminate).

Mexico, Valley of Mexico, 1897, *C. G. Pringle 6610.*

SPECIFIC NAMES APPLIED TO DISTICHLIS

Distichlis, Rafin. in Jour. Phys. **89**: 104. 1819.
ammobia Phil. in Anal. Univ. Chil. **43**: 569. 1873 (South America).
araucana R. Phil. Anal. Univ. Chil. **94**: 162. 1896 (South America).
condensata Hemsl. Biol. Centr. Am. Bot. **3**: 578. 1882–1886 (based on *Megastachya condensatum*) (Mexico) = *Poa* ′
dentata Rydb. Bull. Torrey Club **34**: 536. 1909 (Washington, Sandberg & Leiberg 463) = *D. spicata* var. *stricta*.
distichophylla (Labill.) Fassett. Rhodora **27**: 71. 1925 (based on *Uniola distichophylla*).
hirta Phil. Anal. Univ. Chil. **43**: 570. 1873 (South America).
humilis Phil. Anal. Mus. Nac. Chile, Bot. 86, 1891 (South America).
laxiflora Hackel apud Stuckert in An. Mus. Nac. Buenos Aires **21**: 141. 1911 (South America).
marginata Phil. Anal. Mus. Nac. Chile 86. 1891 (South America).
maritima Benth. Fl. Austral. **7**: 637. 1878 (Australia) *D. distichophylla*.
maritima Rafin. Jour. Phys. **89**: 104. 1819 (based on *Uniola maritima*) = *D. spicata*.
maritima var. *laxa* Holm. Bot. Gaz. **16**: 277. 1891 (Utah) = *D. spicata* var. *stricta*.
maritima var. *stricta* Thurb., in S. Wats., Bot. Calif. **2**: 306. 1880 (based on *Uniola stricta*).
mendocina Phil. Sert. Mend. Alt. 51 (South America).
misera Phil. Anal. Mus. Nac. Chile 86 1891 (South America).
multinervosa Piper. Biol. Soc. Wash. Proc. **18**: 147. 1905 = *Vaseyochloa multinervosa*.
nodosa Rafin. Jour. Phys. **89**: 104. 1819 (based on *Festuca distichophylla* and *F. triticea*) = *Poa michauxii*.
palmeri Fasset ex I. M. Johnston in Proc. Calif. Acad. Sci. Ser. IV. **12**: 984. 1924 = *Uniola palmeri*
prostrata (H.B.K.) E. Desv. in C. Gay, Fl. Chil. **6**: 398. 1853 (based on *Poa prostrata*) (South America)
scoparia (Kunth) Arech. Gram. Urug. 397. tab. 58. 1894 (based on *Poa scoparia*) (South America).
spicata (L.) Greene. Bull. Calif. Acad. **2**: 7. 415. 1887 (based on *Uniola spicata*).
spicata var. *humilis* (Phil.) O. Ktze. Rev. Gen. 3, pt **2**: 350. 1898 (South America).
spicata var. *laxa* Vasey, Beal, Grasses N. Am. **2**: 519. 1896 (Utah, *Tracy* in 1887) = *D. spicata* var. *stricta*.
spicata var. *marginata* (Phil.) O. Ktze. Rev. Gen. Pl. 3, pt. **2**: 350. 1898 (South America).
spicata var. *mendozina* Hack. Anal. Mus Nac. Buenos Aires ser. 3, **6**: 513. 1906 (South America).
spicata stricta Scribn. Mem. Torrey Club **5**: 51. 1894 (based on *Uniola stricta*) = *D. spicata* var. *stricta*.
spicata var. *thalassica* (H.B.K.) Ktze. Rev. Gen. 3, pt. **2**: 350. 1898 (South America).
stricta Rydb. Bull. Torrey Club. 602. 1905 (based on *Uniola stricta*).
stricta var. *laxa* Fassett (spalm. Fawcett) & West ex Munz, Man. South. Cal. 52. 1935 (based on *D. maritima* var *laxa*) *D. spicata* var. *stricta*.
tenuifolia Phil. Anal. Univ. Chil. **94**: 162. 1896 (South America).
texana Scribn. in U. S. Dept. Agr. Bull. Agrost. Circ. **16**: 2. 1899 (based on *Poa texana*).
thalassica (H.B.K.) E Desv. in C. Gay, Fl. Chil. **6**: 397. 1853 (South America) (based on *Poa thalassica*).
thalassica var. *mendocina* Kurtz. Bol. Acad. Nac. Cienc. Cordoba **15**: 521. 1897 (South America).
viridis R. Phil. Anal. Univ. Chile **94**: 163. 1896 (South America).
volckmanni Phil. Anal. Univ. Chil. **43**: 571. 1873 (South America).

DIVISION OF AGRONOMY, UNIVERSITY OF CALIFORNIA
DAVIS, CALIFORNIA

Literature Cited

Fassett, N. C. 1925. Notes on *Distichlis.* Rhodora **27**: 67–72.

Gray, A. 1871. S. Wats., Bot. King's Expl. 385.

Hitchcock, A. S. 1935. Manual of Grasses of the United States. U. S. Dept. Agr. Misc. Publ. 200: 175–179.

Holm, T. 1891. A study of some anatomical characters of North American Gramineae. II. *Distichlis* and *Pleuropogon.* Bot. Gaz. **16**: 277–281.

Rafinesque, C. S. 1819. Prodrome: Des nouveaux genres de plantes observes in 1817 et 1818 dans l'interieur des États-Unis d'Amérique. Jour. Phys. **89**: 103.

Reeder, J. R. 1943. The status of *Distichlis dentata.* Bull. Torrey Club **70**: 53–57.

Rydberg, P. A. 1909. *Distichlis dentata* sp. nov. Bull. Torrey Club **36**: 536.

Scribner, F. L. 1894. List of the Pteridophyta and Spermatophyta growing without cultivation in northeastern North America: Gramineae. Mem. Torrey Club **5**: 51.

Steyermark, J. A. 1940. The first recorded occurrence of *Distichlis spicata* in the central interior of the United States. Rhodora **42**: 22–24.

Stebbins, G. L., Jr. & Love, R. M. 1941. A cytological study of California forage grasses. Am. Jour. Bot. **28**: 371–382.

Thurber, G. 1880. Gramineae. *In* Sereno Watson, Botany of California **2**: 253–328.

Torrey, J. 1824. Ann. Lyc. N. Y. **I**: 155.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

PLANT TAXONOMY AND FLORISTICS
(exclusive of fungi)

Aellen, P. & Just, T. Key and synopsis of the American species of the genus *Chenopodium* L. Am. Midl. Nat. **30:** 47–76. *1 f.* Jl [S] 1943.

Bailey, L. H. *Brahea*, and an *Erythea*. Gentes Herb. **6:** 177–197. *f. 87–100.* Au 1943.

Bailey, L. H. New palms in Panama, and others. Gentes Herb. **6:** 199–264. *f. 101–139.* Au 1943.

Bailey, L. H. Species Batorum. The genus *Rubus* in North America north of Mexico. VI. Section 7 Cuneifolii. Ashen Blackberries. Sand Blackberries. Gentes Herb. **5:** 425–461. *f. 192–210.* 31 Au 1943.

Bakewell, A. Botanical collections of the Wood Yukon Expedition of 1939–1941. Rhodora **45:** 305–316. 10 Au 1943.

Barbour, W. R. Note on *Vantanea Barbourii* Standley. Trop. Woods **75:** 7, 8. 1 S 1943.

Bartram, E. B. Additions to the moss flora of northern Chile. Farlowia **1:** 191–194. *f. 1–5.* Jl 1943.

Bartram, E. B. Burma mosses. Farlowia **1:** 171–189. Jl 1943.

Batalla de Rodriguez, M. A. Estudio de las plantas cultivadas en la region de Izucar de Matamoros, Pue. An. Inst. Biol. [Mexico] **13:** 463–491. *f. 1–4.* 1942 [Jl 1943].

Beetle, A. A. Studies in the genus *Scirpus* L. VI. The section Schoenoplectus Palla. Am. Jour. Bot. **30:** 395–401. Je [26 Jl] 1943.

Blake, S. F. Ten new American Asteraceae. Jour. Wash. Acad. **33:** 265–272. 15 S 1943.

Borsini, O. E. Valerianaceas de Tucuman. Lilloa **8:** 353–377. *pl. 1–12.* 27 My 1943.

Calvey, M. E. A study of a few of the medicinal plants found in Cattaraugus County, N. Y. III. Sci. Stud. St. Bonaventure Coll. **11**[4]: 5–8, 28. Je 1943.

Clausen, R. T. *Sedum hirsutum.* Desert **15:** 90–94. *2 f.* Jl–Au 1943.

Clausen, R. T. & Uhl, C. H. Revision of *Sedum Cockerellii* and related species. Brittonia **5:** 33–46. *f. 1–20.* S 1943.

Clokey, I. W. Notes on the flora of the Charleston Mountains, Clark County, Nevada. V. Cactaceae. Madroño **7:** 67–76. *pl. 4, 5.* 29 Jl 1943.

Coker, W. C. *Magnolia cordata* Michaux. Jour. Elisha Mitchell Soc. **59:** 81–88. *pl. 17–20 f. 1–6.* Jl 1943.

Core, E. L. The genus *Scleria* in extratropical South America. Lilloa **8:** 535–544. 27 My 1943.

Correll, D. S. The genus *Habenaria* in western North America. Leafl. West. Bot. **3:** 233–247. 7 Jl 1943.

Cory, V. L. *Asplenium Palmeri* in Texas. Am. Fern Jour. **33:** 111, 112. Jl–S 1943.

Cory, V. L. The wild cherry of the Carrizo Sands of Texas. Rhodora **45:** 325–327. 10 Au 1943.

Croizat, L. The concept of inflorescence. Bull. Torrey Club **70:** 496–509. *f. 1–15.* 1 S 1943.

Croizat, L. New families. Cactus & Succ. Jour. **15:** 64. My 1943.

Croizat, L. What is the trinomial Typicus? II. Bull. Torrey Club **70:** 406–417. 12 Jl 1943.

Cronquist, A. The legitimacy of *Thalictrum polycarpum* Wats. Madroño **7:** 83. 29 Jl. 1943.

Cronquist, A. Noteworthy plants from Idaho. II. Madroño **7:** 77–82. 29 Jl 1943.

Cronquist, A. The varieties of *Astragalus decumbens.* Leafl. West. Bot. **3:** 250–254. 7 Jl 1943.

Daniel, H. Cordoncillos y Curares. Univ. Antioquia 58: 223–232. Ap–My 1943.

Degener, O. *Stenogyne Sherffii* Degener, a new mint from Hawaii. Brittonia **5:** 58, 59. *f. 1.* 22 S 1943.

Eastwood, A. Some Alpine *Castillejas* from the High Sierra of California. Am. Midl. Nat. **30:** 40–46. *1 pl.* Jl [S] 1943.

Eastwood, A. Variations in *Castilleja plagiotoma.* Leafl. West. Bot. **3:** 248, 249. 7 Jl 1943.

Fassett, N. C. Another driftless area endemic. Bull. Torrey Club **70:** 398, 399. 12 Jl 1943.

Fassett, N. C. The validity of *Juniperus virginiana* var. *crebra.* Am. Jour. Bot. **30:** 469–477. *f. 1–31.* Jl [Au] 1943.

Fernald, M. L. *Centaurea nervosa* in America. Rhodora **45:** 331, 332. 10 Au 1943.

Fernald, M. L. Contributions from the Gray Herbarium—No. CXLVIII. VIII. Notes on *Hieracium.* Rhodora **45:** 317–325. 10 Au 1943.

Fernald, M. L. Eastern extension of *Cirsium Flodmani.* Rhodora **45:** 356. S 1943.

Fernald, M. L. Minor transfers and forms in *Cirsium.* Rhodora **45:** 353, 354. S 1943.

Fernald, M. L. Our albino Lupine. Rhodora **45:** 356. S 1943.

Fernald, M. L. Our varieties of *Trifolium pratense.* Rhodora **45:** 331. 10 Au 1943.

Fernald, M. L. *Trifolium hybridum* and its var. *elegans.* Rhodora **45:** 331. 10 Au 1943.

Fosberg, F. R. Notes on plants of the Pacific Islands. III. Bull. Torrey Club **70:** 386–397. 12 Jl 1943.

Fosberg, F. R. The Polynesian species of *Hedyotis* (Rubiaceae). Bishop Mus. Bull. 174: i, 1–102p. *pl. 1–4.* 5 Ap 1943.

Frye, T. C. & Clark, L. Hepaticae of North America. Part II. Univ. Wash. Publ. Biology **6:** 163–336. *illustr.* 25 Jl 1943.

Giles, N. H. Studies of natural populations of *Cuthbertia graminea* in the Carolinas. Jour. Elisha Mitchell Soc. **59:** 73–80. *f. 1, 2.* Jl 1943.

Gilly, C. An Afro-South American Cyperaceous complex. Brittonia **5:** 1–20. *f. 1.* 20 S 1943.

Gleason, H. A. Contributions of the Torrey Botanical Club to the development of taxonomy. Torreya **43:** 35–43. *f. 1* Jl [27 Au] 1943.

Goodwin, R. H. Check list and index to the Cyperaceae of Monroe County, New York. 1–20. Rochester, New York. The author. Je 1943.

Gundersen, A. Flower forms and groups of Dicotyledons. Bull. Torrey Club **70:** 510–516. *pl. 3, f. 1* S 1943.

Haglund, G. *Taraxacum* in arctic Canada (East of 100° W.) (Introduction by Artheme Dutilly, O.M.I.) Rhodora **45:** 337–343. S 1943.

Harlow, R. C. Is *Polypodium virginianum* f. *deltoideum* a constant form? Am. Fern Jour. **33:** 105, 106. Jl–S 1943.

Hayden, A. A botanical survey in the Iowa Lake region of Clay and Palo Alto counties. Iowa Jour. Sci. **17:** 277–415. *f. 1–38.* Ap 1943.

Heady, H. F. Annotated list of the mosses of the Huntington forest. Roosevelt Wildlife Bull. **8:** 41–58. Je 1943.

Hoover, R. F. Observations on Californian plants—III. Leafl. West Bot. **3:** 254–256. 7 Jl 1943.

Howard, R. A. Studies of the Icacinaceae—VI. *Irvingbaileya* and *Codiocarpus*, two new genera of the Icacineae. Brittonia **5:** 47–57. *f. 1–3.* S 1943.

Howard, R. A. Studies of the Icacinaceae—VII. A revision of the genus *Medusanthera* Seeman. Lloydia **6:** 133–143. *pl. 1.* Je 1943. VIII. Brief notes of some Old World genera. 144–154. *pl 1–3.*

Howell, J. T. Sertulum Greeneanum. Am. Midl. Nat. **30:** 6–39. Jl [S] 1943.

Hume, H. H. *Zephranthes gracilis* Herb. and *Zephranthes minima* Herb. Am. Jour. Bot. **30:** 501–504. *f. 1–5.* Jl [Au] 1943.

Jaramillo, R. El milpesos, monografias botanicas. Univ. Antioquia 58: 215–222. Ap–My 1943.

Jenkins, M. T. A new locality for teosinte in Mexico. Jour. Hered. **34:** 206. *f. 7.* Jl [S] 1943.

Johnson, J. H. Peruvian lime secreting algae from the Guadalupe Mountains, New Mexico. Bull. Geol. Soc Am **53:** 195–226. *pl. 1–7* + *f. 15.* 1 F 1942.

Johnston, I. M. Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango, I. Jour. Arnold Arb. **24:** 306–339. Jl 1943.

Jones, C. H. Additions to the revised catalogue of Ohio vascular plants. XI. Ohio Jour. Sci. **43:** 186–192. Jl 1943.

Jones, C. H. Studies in Ohio floristics. II. Rare plants of Ohio. Castanea **8:** 81–108. My–O [Au] 1943.

Jones, G. N. A new form of *Prunus virginiana* from Indiana and Illinois. Rhodora **45:** 354, 355. S 1943.

Krukoff, B. A. & Moldenke, H. N. Supplementary notes on American Menispermaceae—III. Bull. Torrey Club **70:** 400–406. 12 Jl 1943.

Krukoff, B. A. & Monachino, J. Supplementary notes on the American species of *Strychnos*—I. Brittonia **5:** 21–24. S 1943.

Leonard, E. C. Three new Acanthaceae from Panama. Proc. Biol. Soc. Wash. **56:** 53–56. 16 Je 1943.

Li, Hui-Lin Notes on the flora of Indo-China. Jour. Arnold Arb. **24:** 362–374. Jl 1943.

Li, Hui-Lin On the Sino-Himalayan species of *Shortia* and *Berneuxia*. Rhodora **45**: 333–337. S 1943.

McVaugh, R. Botanical collections of the La Plata expedition of 1853–1855. Brittonia **5**: 64–79. S 1943.

McVaugh, R. The status of certain anomalous native crabapples in eastern United States. Bull. Torrey Club **70**: 418–429. *f. 1–3*. 12 Jl 1943.

Martinez, M. Tres especies nuevas Mexicanas del genero *Abies*. An. Inst. Biol. [Mexico] **13**: 621–634. *f. 1–10*. 1942 [Jl 1943].

Mathias, M. E. & Constance, L. A new species of *Tauschia* from the state of Washington. Madroño **7**: 65–67. *f. 1*. 29 Jl 1943.

Merrill, E. D. An attempt to complete the record. Brittonia **5**: 25–32. S 1943.

Merrill, E. D. An index to Rafinesque's published technical names for the cellular cryptogams. Farlowia **1**: 245–262. Jl 1943.

Merrill, E. D. New names for ferns and fern allies proposed by C. S. Rafinesque, 1806–1838. Am. Fern Jour. **33**: 97–105. Jl–S 1943.

Merrill, E. D. Some economic aspects of taxonomy. Torreya **43**: 50–64. Jl [27 Au] 1943.

Meyer, T. Las Asclepiadaceas Argentinas de los generos *Amblystigma* y *Nautonia*. Lilloa **8**: 379–394. *1 pl.* + *f. 1–4*. 27 My 1943.

Miranda, F. Nuevas fanerogamas del S. O. del Estado de Puebla. An. Inst. Biol. [Mexico] **13**: 451–462. *f. 1–5*. 1942 [Jl 1943].

Moldenke, H. N. Contributions to the flora of extratropical South America. IV. Lilloa **8**: 397–435. 27 My 1943.

Monachino, J. Reduction of *Castelaria Brittonii* Small. Trop. Woods **75**: 4, 5. 1 S 1943.

Moran, R. *Dudleya Anthonyi*. Desert **15**: 86–89. *f. 1–4*. Jl–Au 1943.

Muenscher, W. C. *Potamogeton spirillus* may grow as an annual. Rhodora **45**: 329, 330. 10 Au 1943.

O'Donell, C. A. & Lourteig, A. Hippomaneae Argentinae (Euphorbiaceae). Lilloa **8**: 545–592. *pl. 1–6* + *f. 1–14*. 27 My 1943.

Papenfuss, G. F. Notes on algal nomenclature. II. *Gymnosorus* J. Agardh. Am. Jour. Bot. **30**: 463–468. *f. 1–15*. Jl [Au] 1943.

Patrick, R. The diatoms of Linsley Pond, Connecticut. Proc. Acad. Nat. Sci. Phil. **95**: 53–110. *pl. 11, 12*. 30 Jl 1943.

Pennell, F. W. The Scrophulariaceae of the western Himalayas. Acad. Nat. Sci. Phil. Monograph **5**: *i–vii*, 1–163. *pl. 1–25*. 10 S 1943.

Pennell, F. W. A second summary of the Scrophulariaceae of New Guinea. Jour. Arnold Arb. **24**: 243–274. *pl. 1–5*. Jl 1943.

Pennell, F. W. To the Páramo de Chaquiro. Am. Fern Jour. **33**: 81–96. Jl–S 1943.

Perry, B. A. Chromosome number and phylogenetic relationships in the Euphorbiaceae. Am. Jour. Bot. **30**: 527–543. *f. 1–9*. Jl [Au] 1943.

Porter, C. L. The genus *Amphipappus* Torr. and Gray. Am. Jour. Bot. **30**: 481–483. *f. 1*. Jl [Au] 1943.

Porter, C. L. A new species of *Sphaeralcea* from New Mexico. Bull. Torrey Club **70**: 531, 532. *f. 1, 2*. 1 S 1943.

Record, S. J. Keys to American woods. Trop. Woods **73**: 23–42. 1 Mr 1943. **74**: 17–43. 1 Je 1943. **75**: 8–26. 1 S 1943.

Rickett, H. W. The inflorescence of *Crataegus*. Bull. Torrey Club **70**: 489–495. *f. 1, 2*. 1 S 1943.

Rivera Morales, I. Estudio botanico e historico acerca del "palo copado" *Quararibea funebris* (Llave) Standl. An. Inst. Biol. [Mexico] **13:** 499–502. *1 f.* 1942 [Jl 1943].

Rivera Morales, I. & Miranda, F. Nombres vulgares de plantas en el S. O. de Estado de Pueble. An. Inst. Biol. [Mexico] **13:** 493–498. 1942 [Jl 1943].

Rodrigo, A. del P. Una nueva Malvacea del genero *Sida*. *Sida lilloana* nov. sp. Lilloa **8:** 437–439. *1 pl. + f. a–h.* 27 My 1943.

Ruiz O., M. Estudio de dos especies de hepaticas encontradus en Itzocan de Matamoros, Pue. An. Inst. Biol. [Mexico] **13:** 397–403. *f. 1, 2.* 1942 [Jl 1943].

Schweinfurth, C. A new South American *Lycomormium*. Am. Orchid Soc. Bull. **12:** 134–136. *1 pl.* 3 S 1943.

Schweinfurth, C. A Peruvian novelty in *Catasetum*. Am. Orchid Soc. Bull. **12:** 100. *pl. 1.* 4 Au 1943.

Shaver, J. M. The filmy and polypody ferns in Tennessee. Jour. Tenn. Acad. **18:** 215–222. *f. 10–13.* Jl 1943.

Shaver, J. M. New occurrences of *Dryopteris Clintoniana* in Tennessee. Am. Fern Jour. **33:** 107–109. Jl–S 1943.

Shinners, L. H. The genus *Aster* in Nova Scotia. Rhodora **45:** 344–351. S 1943.

Smith, A. C. *Killipiella*, a new Colombian genus of Vacciniaceae. Jour. Wash. Acad. **33:** 242–244 *f. 1.* 15 Au 1943.

Smith, A. C. Studies of Pacific Island plants, II. Notes on the Pacific species of *Piper*. Jour. Arnold Arb. **24:** 347–361. Jl 1943.

Smith, A. C. Studies on Pacific Island plants—III. New and noteworthy flowering plants from Fiji Bull. Torrey Club **70:** 533–549. 1 S 1943.

Stehlé, H. La vegetation muscinales des Antilles Francaises et son interet dans la valorisation sylvicole. Carib. Forester **4:** 164–182. Jl 1943.

Standley, P. C. A Costa Rican species of *Vantanea*, of the family Humiriaceae, a group new to Central America. Trop. Woods **75:** 5, 6. 1 S 1943.

Stout, A. B. *Hemerocallis altissima* Stout sp. nov. The Tsu kin shan daylily. Herbertia **9:** 103–106. *f. 71–76.* My 1943.

Svenson, H. K. Modern taxonomy and its relation to geography. Torreya **43:** 44–49. Jl [Au] 1943.

Vecchierello, H. Hepaticae or liverworts mentioned in David F. Day's Catalogue of the plants of western New York and a Revision of the names to bring the list in conformity with current nomenclature. Sci. Stud. St. Bonaventure Coll. **11**[4]: 9. Je 1943.

Vecchierello, H. List of mosses mentioned by David F. Day in his Catalogue of plants of Western New York, brought up to date with reference to terminology, etc. Sci. Stud. St. Bonaventure Coll. **11**[4]: 11–14. Je 1943.

Waterfall, U. T. A new species of *Haplopappus* from southwestern Texas. Rhodora **45:** 351–353. S 1943.

Weatherby, C. A. Valid and legitimate names—and *Thalictrum polycarpum* S. Wats. Madroño **7:** 83–85. 29 Jl 1943.

Wherry, E. T. *Microsteris*, *Phlox*, and an intermediate. Brittonia **5:** 60–63. *f. 1.* S 1943.

Woodson, R. E. A new *Amsonia* from the Ozarks of Arkansas. Rhodora **45:** 328, 329. 10 Au 1943.

Yuncker, T. G. *Cuscuta Flossdorfii* Hicken. Lilloa **8:** 395, 396, 27 My 1943.

MORPHOLOGY

(including anatomy, and cytology in part)

(See also under Taxonomy: **Perry**; under Mycology and Phytopathology: **Woods & DuBuy**)

Bailey, I. W. & Nast, C. G. The comparative morphology of the Winteraceae. I. Pollen and stamens. Jour. Arnold Arbor. **24:** 340–346. *pl. 1–3.* Jl 1943.

Bannan, M. W. Wood structure of *Ryania.* Am. Jour. Bot. **30:** 351–355. *f. 1–37.* My [4 Je] 1943.

Berger, C. A. & Witkus, E. R. A cytological study of c-mitosis in the polysomatic plant *Spinacia oleracea,* with comparative observations on *Allium cepa.* Bull. Torrey Club **70:** 457–466. *pl. 1, 2 + f. 17, 18.* 1 S 1943.

Carlson, M. C. The morphology and anatomy of *Calopogon pulchellus.* Bull. Torrey Club **70:** 349–368. *f. 1–36.* 12 Jl 1943.

Cheadle, V. I. Vessel specialization in the late metaxylem of the various organs in the Monocotyledoneae. Am. Jour. Bot. **30:** 484–490. *f. 1–8.* Jl [Au] 1943.

Crafts, A. S. Vascular differentiation in the shoot apices of ten coniferous species. Am. Jour. Bot. **30:** 382–393. *f. 1–9.* My [4 Je] 1943.

Cross, G. L. The shoot apices of *Athrotaxis* and *Taiwania.* Bull. Torrey Club **70:** 335–358. *f. 1–6.* 12 Jl 1943.

Darrow, R. A. Vegetative and floral growth of *Fouquieria splendens.* Ecology **24:** 310–322. *f. 1–6.* Jl 1943.

Ernst-Schwarzenbach, M. The sexual dimorphism of the tropical mosses of the genus *Macromitrium.* Farlowia **1:** 195–198. *f. 1–5.* Jl 1943.

Esau, K. Ontogeny of the vascular bundle in *Zea mays.* Hilgardia **15:** 327–356. *pl. 1–10 + f. 1–4.* Ap 1943.

Esau, K. Vascular differentiation in the pear root. Hilgardia **15:** 299–311. *pl. 1–10.* Ap 1943.

Gaiser, L. O., Sutherland, M. & Moore, R. Cytological studies in *Martynia louisiana.* Am. Jour. Bot. **30:** 543–551. *f. 1–16.* Jl [Au] 1943.

Isenberg, I. H. The anatomy of redwood bark. Madroño **7:** 85–91. *pl. 6–18.* 29 Jl 1943.

Johnson, M. A. Foliar development in *Zamia.* Am. Jour. Bot. **30:** 366–378. *f. 1–51.* My [4 Je] 1943.

Kemp, M. Morphological and ontogenetic studies on *Torreya californica* Torr. I. The vegetative apex of the megasporangiate tree. Am. Jour. Bot. **30:** 504–517. *f. 1–17.* Jl [Au] 1943.

Knobloch, I. W. Morphological variation and cytology of *Bromus inermis.* Bull. Torrey Club **70:** 467–472. *f. 1–3.* 1 S 1943.

Moseley, M. F. Contributions to the life history, morphology and phylogeny of *Widdringtonia cupressoides.* Lloydia **6:** 109–132. *f. 1–27.* Je 1943.

Sharp, L. W. Fundamentals of cytology. *i–x,* 1–270. *illustr.* McGraw-Hill. 1943.

Shull, J. M. Diversity of form in daylilies. Herbertia **9:** 156–161. *pl. 230, 231 + f. 79.* My 1943.

Sinnott, E. W. Cell division as a problem of pattern in plant development. Torreya **43:** 29–34. *f. 1–4.* Jl [27 Au] 1943.

Smith, E. C. A study of cytology and speciation in the genus *Populus* L. Jour. Arnold Arbor. **24:** 275–305. *pl. 1–4.* Jl 1943.

Stone, E. L. & Stone, M. H. Dormant buds in certain species of *Pinus.* Am. Jour. Bot. **30:** 346–351. *f. 1–10.* My [4 Je] 1943.

Stone, E. L. & Stone, M. H. "Dormant" versus "adventitious" buds. Science **98:** 62. 16 Jl 1943.

Wetmore, R. H. Leaf-stem relationships in the vascular plants. Torreya **43:** 16–28. *f. 1–8.* Jl [27 Au] 1943.

PLANT PHYSIOLOGY

Addicott, F. J. Pollen germination and tube growth in *Milla* as affected by pure growth substances. Herbertia **9:** 133–135. My 1943.

Barton, L. V. Effect of moisture fluctuations on the viability of seeds in storage. Contrib. Boyce Thompson Inst. **13:** 35–45. *f. 1, 2.* Ap–Je 1943.

Barton, L. V. The storage of citrus seeds. Contrib. Boyce Thompson Inst. **13:** 47–55. Ap–Je 1943.

Bernstein, L. Amylases and carbohydrates in developing maize endosperm. Am. Jour. Bot. **30:** 517–526. *f. 1–4.* Jl [Au] 1943.

Berry, L. J. & Hoyt, R. C. Polarization and stimulation of the onion root by direct current. Plant Physiol. **18:** 372–396. *f. 1–10.* Jl [Au] 1943.

Bonner, J. & Dorland, R. Some observations concerning riboflavin and pantothenic acid in tomato plants. Am. Jour. Bot. **30:** 414–418. *f. 1.* Je [26 Jl] 1943.

Briggs, G. B. Effect of boron in the substrate on the rate of nitrate absorption and on nitrogen distribution in Nasturtium. Plant Physiol. **18:** 415–432. *f. 1.* Jl [Au] 1943.

Burkholder, P. R. & Moyer, D. Vitamin deficiencies of fifty yeasts and molds. Bull. Torrey Club **70:** 372–377. 12 Jl 1943.

Denny, F. E. Inactivation of the browning system in dried apples. Contr. Boyce Thompson Inst. **13:** 57–63. *f. 1.* Ap–Je 1943.

Denny, F. E. & Thornton, N. C. Effect of post-harvest pre-storage conditions on the rate of development of sugar in potato tubers during subsequent cold storage. Contr. Boyce Thompson Inst. **13:** 65–71. Ap–Je 1943.

Doneen, L. D. & MacGillivray, J. H. Germination (emergence) of vegetable seed as affected by different soil moisture conditions. Plant Physiol. **18:** 524–529. *f. 1.* Jl [Au] 1943.

Fan, C. S., Stauffer, J. F. & Umbreit, W. W. An experimental separation of oxygen liberation from carbon dioxide fixation in photosynthesis by *Chlorella.* Jour. Gen. Physiol. **27:** 15–28. *f. 1–5.* 20 S 1943.

Frazier, J. C. Food reserve depletion and synthesis in field bindweed, *Convolvulus arvensis* L., as related to 7-day and 14-day intervals of cultivation. Plant Physiol. **18:** 315–323. Jl [Au] 1943.

Galston, A. W. The isolation, agglutination and nitrogen analysis of oat chloroplasts. Am. Jour. Bot. **30:** 331–334. *f. 1.* My [4 Je] 1943.

Hedrick, J. A. & Alexopoulos, C. J. A further note on the production of thiamine by *Actinomyces.* Bull. Torrey Club **70:** 369–371. 12 Jl 1943.

Kramer, P. J. & Wetmore, T. H. Effects of defoliation on cold resistance and diameter growth of broadleaved evergreens. Am. Jour. Bot. **30:** 428–431. Je [26 Jl] 1943.

Leonard, R. H. & Dustman, R. B. Sugars in relation to color and thiocyanate spray in apples. Plant Physiol. **18:** 488–497. Jl [Au] 1943.

Lineberry, R. A. & Burkhart, L. Nutrient deficiencies in the strawberry leaf and fruit. Plant Physiol. **18:** 324–333. *f. 1–7.* Jl [Au] 1943.

Lyon, C. J. Water supply and the growth rates of conifers around Boston. Ecology **24:** 329–344. *f. 1–4.* Jl 1943.

Marczynzski, R. Studies on the nutrition of *Collybia velutipes* (Curt.) Quel. (Homobasidiomycetes, Agaricales). Am. Midl. Nat. **30:** 164–170. Jl [S] 1943.

Mandels, G. R. A quantitative study of chlorosis in *Chlorella* under conditions of sulphur deficiency. Plant Physiol. **18:** 449–462. *f. 1–10.* Jl [Au] 1943.

Meyer, B. S. *et al.* Effect of depth of immersion on apparent photosynthesis in submersed vascular aquatics. Ecology **24:** 393–399. Jl 1943.

Meyer, S. L. & Ford, C. H. Influence of the hydrogen-ion concentration of the substrata on the development of leafy moss plants. Plant Physiol. **18:** 530–533. Jl [Au] 1943.

Moinat, A. D. Nutritional relationships of boron and indoleacetic acid in head lettuce. Plant Physiol. **18:** 517–523. *f. 1–2.* Jl [Au] 1943.

Noecker, N. L. & Reed, M. Observations on the vitamin requirements of *Stereum frustulosum* (Pers.) Fr. Am. Midl. Nat. **30:** 171–174. Jl [S] 1943.

Osterhout, W. J. V. Nature of the action current in *Nitella.* V. Partial response and the all-or-none law. Jour. Gen. Physiol. **27:** 61–67. *pl. 1 f. 1, 2.* 20 S 1943.

Pratt, R. Studies on *Chlorella vulgaris.* VII. Influence of the age of the culture on the rates of photosynthesis and respiration. Am. Jour. Bot. **30:** 404–408. *f. 1–6.* Je [26 Jl] 1943.

Richards, O. W. & Kavanagh, A. J. The analysis of the relative growth gradients and changing form of growing organisms illustrated by the tobacco leaf. Am. Nat. **77:** 385–395. *f. 1–3.* S–O 1943.

Riley, G. A. Physiological aspects of spring diatom flowerings. Bull. Bingham Oceanog. Coll. **8**[4]: 1–53. *f. 1–15.* Je 1943.

Robbins, W. J. Further observations on the specificity of Hypoxanthine for *Phycomyces.* Proc. Nat. Acad. **29:** 201, 202. 15 Jl 1943.

Roberts, R. H. & Struckmeyer, B. E. Blossom induction of the cranberry. Plant Physiol. **18:** 534–536. *f. 1, 2.* Jl [Au] 1943.

Routien, J. B. & Dawson, R. F. Some interrelationships of growth, salt absorption, respiration, and mycorrhizal development in *Pinus echinata* Mill. Am. Jour. Bot. **30:** 440–451. Je [26 Jl] 1943.

Satina, S. & Blakeslee, A. F. Periclinal chimeras in *Datura* in relation to the development of the carpel. Am. Jour. Bot. **30:** 453–462. *f. 1–31.* Jl [Au] 1943.

Schopfer, W. H. Plants and vitamins. Authorized translation by Norbert C. Noecker. *xiv*, 1–293p. *pl. 1–3.* Waltham, Mass., Chronica Botanica. 1943.

Thomas, M. D. *et al.* The utilization of sulphate and sulphur dioxide for the sulphur nutrition of alfalfa. Plant Physiol. **18:** 345–371. *f. 1–5.* Jl [Au] 1943.

Turrell, F. M., Sokoloff, V. P. & Klotz, L. J. Structure and composition of citrus leaves affected with mesophyll collapse. Plant Physiol. **18:** 463–475. *f. 1–6.* Jl [Au] 1943.

Withrow, R. B. Radiant energy nomenclature. Plant Physiol. **18:** 476–487. Jl [Au] 1943.

Zimmerman, P. W. Present status of "plant hormones." Boyce Thompson Inst. Prof. Pap. **1:** 307–320. *f. 1–5.* F 1943.

GENETICS
(Including cytogenetics)

Allen, C. E. The evolution and determination of sexual characters in the Angiosperm sporophyte. Torreya **43:** 6–15. Jl [27 Au] 1943.

Atkinson, L. R. A preliminary report of fertilization in *Marsilea vestita.* Am. Jour. Bot. **30:** 401–404. *f. 1–9.* Je [26 Jl] 1943.

Beard, F. C. The germination capacity of maize pollen having aberrant nuclei. Bull. Torrey Club **70:** 449–456. *f. 1–5.* 1 S 1943.

Beatty, A. V. The division of the generative nucleus in *Eschscholtzia.* Am. Jour. Bot. **30:** 378–382. *f. 1–12.* My [4 Je] 1943.

Bergner, A. D. Chromosomal interchange among six species of *Datura* in nature. Am. Jour. Bot. **30:** 431–440. *f. 1–3.* Je [26 Jl] 1943.

Brown, M. S. Haploid plants in sorghum. Jour. Hered. **34:** 163–166. *f. 1–3.* Je [Au] 1943.

Cooper, D. C. Haploid-diploid twin embryos in *Lilium* and *Nicotiana.* Am. Jour. Bot. **30:** 408–413. *f. 1–19.* Je [26 Jl] 1943.

Davis, B. M. An amphidiploid in the F_1 generation from the cross *Oenothera franciscana* × *Oenothera biennis,* and its progeny. Genetics **28:** 275–285. *pl. 1, 2 + f. 1.* Jl 1943.

Einset, J. Chromosome length in relation to transmission frequency of maize trisomes. Genetics **28:** 349–364. S 1943.

Horovitz, S. & Marchioni, A. H. Herencia de la resistencia a la langosta en el maiz "Amargo". An. Inst. Fito. Santa Catalina **2:** 27–52. *pl. 8, 9. f. 1–3.* 1942 [1943].

Immer, F. R. & Henderson, M. T. Linkage studies in barley. Genetics **28:** 419–440. S 1943.

Johnson, T. & Newton, M. The inheritance of a mutant character in *Puccinia graminis tritici.* Canad. Jour. Res C **21:** 205–210. *f. 1–7.* Jl 1943.

Keitt, G. W., Langford, M. H. & Shay, J. R. *Venturia inaequalis* (Cke.) Wint. II. Genetic studies on pathogenicity and certain mutant characters. Am. Jour. Bot. **30:** 491–500. *pl. 1–3.* Jl [Au] 1943.

Lesley, M. M. & Lesley, J. W. Hybrids of the Chilean tomato. Sterile and fertile plants of *Lycopersicon Peruvianum* var. *Dentatum* Dun. (*L. Chilense* Dun.) and diploid and tetraploid hybrids with cultivated tomatoes. Jour. Hered. **34:** 199–205. *f. 2–6.* Jl [S] 1943.

Mazoti, L. B. Estudio genetico sobre maices amilaceos de Argentina. An. Inst. Fito Santa Catalina **2:** 17–26. 1942 [1943].

Mehlquist, G. A. L., Blodgett, C. O. & Bruscia, L. Colchicine induced tetraploidy in *Delphinium cardinale.* Jour. Hered. **34:** 187–192 *f. 18, 19.* Je [Au] 1943.

Morgan, D. T. The formation of chromocenters in interkinetic nuclei of maize by knobs and B chromosomes. Jour. Hered. **34:** 195–198. *f. 1.* Jl [Au] 1943.

Myers, W. M. & Hill, H. D. Increased meiotic irregularity accompanying inbreeding in *Dactylis glomerata* L. Genetics **28:** 383–397. S 1943.

Newcomber, E. H. An F_2 colchicine-induced tetraploid cabbage and some comparisons with its diploid progenitor. Jour. Elisha Mitchell Soc. **59:** 69–72. *pl. 13–16.* Jl 1943.

Perak, J. T. *Triticum durum* tetraploide obtenido por colchicina. An. Inst. Fito Santa Catalina **2:** 7, 8. *pl. 1.* 1942 [1943].

Riley, H. P. Cell size in developing ovaries of *Iris hexagona* var. *giganticaerulae.* Am. Jour. Bot. **30:** 356–361. *f. 1–7.* My [4 Je] 1943.

Salomon, E. S. *Sorghum sudanense* (Piper) Stapf tertaploide obtenido por colchicina. An. Inst. Fito Santa Catalina **2:** 13–16. *pl. 6, 7.* 1942 [1943].

Schnack, B. Obtencion de poliploides en *Gaillardia pulchella* Foug., por le accion de la Colchicina. An. Inst. Fito Santa Catalina **2:** 9–12. *pl. 2–5.* 1942 [1943].

Smith, D. C. Intergeneric hybridization of *Triticum* and other grasses, principally *Agropyron.* Jour. Hered. **34:** 219–224. *f. 14.* Jl [S] 1943.

Swanson, C. P. The behavior of meiotic prophase chromosomes as revealed through the use of high temperatures. Am. Jour. Bot. **30:** 422–428. *f. 1–13.* Je [26 Jl] 1943.

Vilkomerson, H. Chromosomes of *Astragalus.* Bull. Torrey Club **70:** 430–435. *f. 1.* 12 Jl 1943.

MYCOLOGY AND PHYTOPATHOLOGY

Andrews, E. A. Seedling blight and root rot of grasses in Minnesota. Phytopathology **33:** 234–239. Mr 1943.

Arndt, C. H. *Phythium ultimum* and the damping-off of cotton seedlings. Phytopathology **33:** 607–611. Jl 1943.

Baker, E. E., Mrak, E. M. & Smith, C. E. The morphology, taxonomy, and distribution of *Coccidioides immitis* Rixford and Gilchrist 1896. Farlowia **1:** 199–244. *pl. 1–8.* Jl 1943.

Barnett, H. L. The development and structure of *Longia texensis.* Mycologia **35:** 399–408. *f. 1–3.* 1 Au 1943.

Bisby, G. R. Geographical distribution of fungi. Bot. Rev. **9:** 466–482. Jl 1943.

Blodgett, E. C. Rasp leaf of cherry. Phytopathology **33:** 620–622. *f. 1.* Jl 1943.

Chilton, S. J. P., Henson, L. & Johnson, H. W. Fungi reported on species of *Medicago, Melilotus,* and *Trifolium.* U. S. Dept. Agr. Misc. Publ. 499: 1–152. Jl 1943.

Condit, I. J. & Horne, W. T. Mosaic spots of fig fruits. Phytopathology **33:** 719–723. *f. 1, 2.* Au 1943.

Cummins, G. B. Descriptions of tropical rusts—VI. Bull. Torrey Club **70:** 517–530. *f. 1–12.* 1 S 1943.

Cummins, G. B. Uredinales from the northwest Himalaya. Mycologia **35:** 446–458. *f. 1–7.* 1 Au 1943.

Dimock, A. W. Powdery mildew on ribbon-bush (*Homalocladium platycladum* Bailey). Phytopathology **33:** 745, 746. *f. 1.* Au 1943.

Dodge, B. O. & Rickett, H. W. Diseases and pests of ornamental plants. *i–xi,* 1–638p. *illust.* J. Cattell, Lancaster, Pa. 1943.

Doolittle, S. P. Tomato diseases. U. S. Dept. Agr. Farmers' Bull. 1934: 1–83. *f. 1–47.* Je 1943.

Forbes, I. L. & Mills, P. J. Disappearance of virus from mosaic-diseased sugarcane plants. Phytopathology **33:** 713–718. Au 1943

Fulton, R. W. The sensitivity of plant viruses to certain inactivators. Phytopathology **33:** 674–682. Au 1943.

Gottlieb, D. & Hart, H. Growth substances and the rust fungi. Phytopathology **33:** 724–728. Au 1943.

Griffith, R. B. A leaf disease of Kentucky bluegrass. Phytopathology **33:** 745. Au 1943.

Groves, J. W. *Dermatea bicolor* on *Amelanchier.* Mycologia **35:** 459–464. *f. 1–3.* Au 1943.

Hamilton, J. M. & Weaver, L. O. Freezing preservation of fungi and fungus spores. Phytopathology **33:** 612, 613. *f. 1.* Jl 1943.

Hansen, H. N. & Snyder, W. C. The dual phenomenon and sex in *Hypomyces solani* f. *cucurbitae.* Am. Jour. Bot. **30:** 419–422. *f. 1–3.* Je [26 Jl] 1943.

Harrold, T. J. Histological studies of infections of the cotton hypocotyl by *Glomerella gossypii* and *Fusarium moniliforme*. Phytopathology **33:** 666–673. *f. 1–5.* Au 1943.

Heald, F. D. Introduction to plant pathology. 2nd ed. *xii*, 1–603. *f. 1–246.* McGraw-Hill, New York. 1943.

Hildebrand, A. A. & Koch, L. W. Rhizopus root rot of sugar beet. Canad. Jour. Res. C **21:** 235–248. *pl. 1, 2 + f. 1–10.* Au 1943.

Holmes, F. O. A tendency to escape tobacco-mosaic disease in derivatives from a hybrid tomato. Phytopathology **33:** 691–697. Au 1943.

Holton, C. S. Chlamydospore germination in the fungus causing dwarf bunt of wheat. Phytopathology **33:** 732–735. *f. 1.* Au 1943.

Jenkins, A. E. & Chupp, C. *Cercospora* on *Morinda Royoc*. Mycologia **35:** 480–482. *f. 1.* 1 Au 1943.

Jenkins, A. E. & Viégas, A. P. Stem and foliage scab of sweet potato (*Ipomoea batatas*). Jour. Wash. Acad. **33:** 244–249. *f. 1, 2.* 15 Au 1943.

Katznelson, H. & Richardson, L. T. The microflora of the rhizosphere of tomato plants in relation to soil sterilization. Canad. Jour. Res. C **21:** 249–255. Au 1943.

Kern, F. D. The importance of taxonomic studies of the fungi. Torreya **43:** 65–77. Jl [27 Au] 1943.

Kern, F. D. & Thurston, H. W. Additions to the Uredinales of Venezuela—II. Mycologia **35:** 434–445. 1 Au 1943.

Kreitlow, K. W. *Ustilago striaeformis*. I. Germination of chlamydospores and culture of forma *agrostidis* on artificial media. Phytopathology **33:** 707–712. *f. 1.* Au 1943.

Kunkel, L. O. Potato witches'-broom transmission by dodder and cure by heat. Proc. Am. Philos. Soc. **86:** 470–475. *f. 1–4.* 8 Jl 1943.

Linder, D. H. A new species of *Phyllactinia*. Mycologia **35:** 465–468. *f. 1.* 1 Au 1943.

Lohman, M. L. & Watson, A. J. Identity and host relations of *Nectria* species associated with diseases of hardwoods in the eastern states. Lloydia **6:** 77–108 *f. 1, 2.* Je 1943.

Lutz, H. J. Injuries to trees caused by *Celastrus* and *Vitis*. Bull. Torrey Club **70:** 436–439. *f. 1–3.* 12 Jl 1943.

McKinney, H. H. Reaction of resistant tobaccos to certain strains of *Nicotiana* virus 1 and other viruses. Phytopathology **33:** 551–568. *f. 1–6.* Jl 1943.

McNair, J. B. Advance in phylogenetic position in the cryptogams as indicated by their fats. Lloydia **6:** 155, 156. *f. 1.* Je 1943.

Martin, W. J. A study of the genetics of *Sorosporium syntherismae* and *Sphacelotheca panici-miliacei*. Phytopathology **33:** 569–585. *f. 1–5.* Jl 1943.

Murrill, W. A. Some southern novelties. Mycologia **35:** 422–433. 1 Au 1943.

Pratt, R. Influence of temperature on the infection of wheat by the powdery mildew *Erysiphe graminis tritici*. Bull. Torrey Club **70:** 378–385. *f. 1, 2.* 12 Jl 1943.

Price, W. C. Severity of curley top in tobacco affected by site of inoculation. Phytopathology **33:** 586–601. *f. 1.* Jl 1943.

Reynard, G. B. "Red ring" of tomato stems caused by an insect, *Cyrtopeltis varians* (Dist.) at Charleston, S. C. Phytopathology **33:** 613–615. *f. 1.* Jl 1943.

Rogers, D. P. & Jackson, H. S. Notes on the synonymy of some North American Thelephoraceae and other resupinates. Farlowia **1:** 263–336. Jl 1943.

Seaver, F. J. Photographs and descriptions of cup-fungi—XXXVIII. The genus *Kriegeria.* Mycologia **35:** 492, 493. 1 Au 1943.

Severin, H. H. P. Breaking in color of flowers of annual *Phlox* caused by the aster-yellows virus. Phytopathology **33:** 741–743. *f. 1.* Au 1943.

Shear, C. L. Mycological notes. VII. Mycologia **35:** 469–476. 1 Au 1943.

Singer, R. A monographic study of the genera *Crinipellis* and *Chaetocalathus.* Lilloa **8:** 441–534. *f. 1–6.* 27 My 1943.

Smith, A. H. & Walters, M. B. A new species of *Tricholoma.* Mycologia **35:** 477–479. 1 Au 1943.

Sprague, R. The genus *Phaeoseptoria* on grasses in the western hemisphere. Mycologia **35:** 483–491. *f. 1–2.* 1 Au 1943.

Thomas, H. R. A nonchromogenic sporulating variant of *Alternaria solani.* Phytopathology **33:** 729–731. *f. 1.* Au 1943.

Vallega, J. Especializacion fisiologica de *Puccinia cornoata avenae,* en Argentina. An. Inst. Fito Santa Catalinia **2:** 53–82. *pl. 10.* 1942 [1943].

Vechierello, H. The list of Myxomycetes mentioned in David F. Day's catalogue. Sci. Stud. St. Bonaventure Coll. **11**[4]: 21. Je 1943.

Virgin, W. J. An unusual bean disease. Phytopathology **33:** 743–745. *f. 1.* Au 1943.

Walter, J. M., May, C. & Collins, C. W. Dutch elm disease and its control. U. S. Dept. Agric. Circ. 677: 1–12. *f. 1–12.* Jl 1943.

Weber, G. F. Southern blight, *Corticium rolfsii,* of potato tubers. Phytopathology **33:** 615–617. *f. 1.* Jl 1943.

Whetzel, H. H. & Solheim, W. G. *Sclerotinia Caricis-ampullaceae,* a remarkable sub-arctic species. Mycologia **35:** 385–398. *f. 1–6.* 1 Au 1943.

White, P. R. & Braun, A. C. A cancerous neoplasm of plants produced by autonomous, bacteria-free crown-gall-tissues. Am. Philos. Soc. Proc. **86:** 467–469. 8 Jl 1943.

Woods, M. W. & DuBuy, H. G. Evidence for the evolution of phytopathogenic viruses from Mitochondria and their derivatives. I. Cytological and genetic evidence. Phytopathology **33:** 637–655. *f. 1–8.* Au 1943.

Wynd, F. L. Metabolic phenomena associated with virus infection in plants. Bot. Rev. **9:** 395–465. Jl 1943.

Young, G. Y. Root rots in storage of deciduous nursery stock and their control. Phytopathology **33:** 656–665. Au 1943.

Zeller, S. M. North American species of *Galeropsis, Gyrophragnium, Longia,* and *Montagnea.* Mycologia **35:** 409–421. *f. 1.* 1 Au 1943.

PALEOBOTANY

Brown, R. W. Jefferson's contribution to paleontology. Jour. Wash. Acad. **33:** 257–259. 15 S 1943.

Fenton, C. L. A new Devonian alga from western Australia. Am. Midl. Nat. **30:** 112. *f. 1.* Jl [S] 1943.

Fenton, C. L. Pre-Cambrian and early Paleozoic algae. Am. Midl. Nat. **30:** 83–111. *f. 1–15.* Jl [S] 1943.

Hansen, H. P. Paleoecology of two sand dune bogs on the southern Oregon Coast. Am. Jour. Bot. **30:** 335–340. *f. 1–3.* My [4 Je] 1943.

Hoskins, J. H. & Cross, A. T. Monograph of the Paleozoic cone genus *Bowmanites* (*Sphenophyllales*). Am. Midl. Nat. **30:** 113–163 *f. 1–40.* Jl [S] 1943.

Kirk, E. A revision of the genus *Steganocrinus.* Jour. Wash. Acad. **33:** 259–265. *f. 1–5.* 15 S 1943.

INDEX TO VOLUME 70

New names and combinations are designated by **bold face** type.

IMPERIAL AGRICULTURAL RESEARCH
INSTITUTE LIBRARY
NEW DELHI.

Date of issue.	Date of issue.	Date of issue.
14.8.57		
10 JUN 1955		
0 JUN 1955		
15.1.60		